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Kathleen Muriel Shaw B Sc.

The measurement of species diversity, and its relationship
to community stability.

Dissertation for the degree of Bachelor of Philosophy

Mathematical Ecology

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Abstract

Species diversity is hard to define either as a single attribute or as two separate concepts of number of species present in a community and the equitability of the distribution of individuals amongst the species. While it is easy to produce a list of conditions that should be satisfied by any measure agreeing with our intuitive conception of equitability, some of these conditions are mutually contradictory. It is hardly surprising therefore that no single measure of diversity or equitability is perfectly satisfactory and that different measures may produce conflicting orderings of the same set of communities. Chapter 1 gives an introductory survey of the various ways of measuring diversity and equitability - by a single function of the species abundances, by a parameter of a distribution fitted to the observed distribution of species abundances, or by defining a partial ordering of communities. I comment on the principles behind a definition of diversity or equitability, and on the ideas to be considered when choosing a suitable measure. In Chapter 2 I first discuss the ways in which the environment may affect the diversity of communities able to live there, and present some of the experimental evidence. Secondly I discuss the possibility that the diversity of a community may affect its ability to survive in a changing environment. Here experimental evidence is sparse and contradictory. Therefore, in Chapter 3, I study this problem further by computer simulation, and show that factors other than diversity play an important part. In my pilot study of only two species the main effect on stability is that of changing the equilibrium number of individuals. No diversity effect could be detected. Perhaps more species are needed, but even a three-species simulation involves considerably more variables if it is to be investigated fully.

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Introduction

When we consider a community of plants and animals living together, we are prompted to consider such questions as 'why should there be just this many species, no more and no fewer?'. The answer will depend on many things - the environment, the nature of the species involved, their interactions with each other, and how abundant each species is. A study of each community separately, considering all the species present and their interactions with each other is theoretically possible but in practice impossibly time-consuming. A general theory relating the number and abundances of species to such factors as the nature of the environment, or the length of time that the community has been free from major disturbance, will arise only from the consideration of some simple measure summarising the structure of the community. It may be possible to measure this structure without considering the identity of all the species present; we can distinguish between a simple community of few species and a more complex community of many species, and the abundances of the species may reflect something of the magnitude of the interactions between the species. This aspect of the community - the number of species present and their relative abundances - is what we mean by species diversity.

In Chapter 1, I consider some of the ways in which we attempt to measure diversity. The crudest measure is simply the number of species present, but a more informative measure will also take into account the relative abundances of the species. We can consider the distribution of abundances among the species present and attempt to fit a theoretical model. We may then be able to use the parameters of this model to measure diversity, or we may wish to use a measure that is independent of any fitted model. Finally, we can try to separate 'diversity' into

its two components of the number of species and the equitability of distribution of abundances among these species.

I discuss some problems in measuring diversity - the question of an exact definition of diversity, and the effects of sample size on the measures of diversity in common use - and I make some suggestions concerning suitable choices of diversity measures.

In Chapter 2, I consider some of the theories relating diversity to other factors - high diversity as a consequence of a favourable environment, the way the diversity of a community changes during ecological succession, and the question of whether a highly diverse community is more or less stable than a community with lower diversity. Stability can mean different things. There is the traditional mathematical concept of stability - the ability of a community to return to its equilibrium position after a small perturbation in species numbers. Most of the work on this subject has been theoretical, relating stability to the number of species. A more interesting question is whether a diverse community is more or less able than a non-diverse one to withstand a shock to the environment. The shock may be a temporary one, such as a single application of fertilizer or insecticide which alters the species abundances considerably but leaves the environment (and hence the equilibrium position) fundamentally unchanged. The many experimental studies on this subject are in general concerned with the link between stability and diversity, not merely stability and number of species.

Alternatively, the shock to the environment may cause a permanent change to the environment, defining a new equilibrium position for the community. There has been little experimental work on this. In Chapter 3, I show how the problem could be approached by computer simulation, confining my attention to the possible link between stability

and equitability. I present a pilot study on two species only, and this is sufficient to bring attention to several unforeseen problems; for example, changing the equilibrium number of individuals in the community has a far greater effect on stability than has the diversity of the community.

1. The measurement of species diversity

1.1 i) Use of the number of species as a diversity index

At its simplest the diversity of a community is just the number of species present in the community. It is known that for most classes of plants and animals the number of species increases from the Poles to the equator; tropical forests are considered to be among the most diverse ecosystems. This trend is repeated among marine animals with greater numbers of species in shallow tropical seas than in shallow northern seas. Another trend among terrestrial creatures is for the number of species to increase with land area - a high diversity on the large continental land masses and a much smaller number of species on small islands. Number of species also appears to increase towards more stable environments: the fauna of the cold deep-sea is very diverse.

1.1 ii) Desirability of including abundance in a measure of diversity

However, to use number of species as a measure of diversity is to ignore much of the information we have about that community. In any natural community some species will be present in large numbers, but the majority will be represented by only a few individuals. Ideally we would like a measure of diversity that takes into account the differing abundances of the species, since a community with many abundant species is likely to behave differently from, and exhibit different interactions between, its species than one with the same number of species but only one which is abundant. A community having more species than another community can be considered as being more diverse, but so can a community in which the species are more or less

equally represented be considered more diverse than a community with the same number of species, but in which one species accounts for 90% of the population and the other species together for only 10% of the population.

1.1 iii) Measures of abundance

In some applications it may be more appropriate to consider aspects of the community other than numbers of individuals. For example, if the community involved is one of plants of widely differing growth forms, say single plantains amongst spreading clumps of grass, biomass will be a more appropriate measure of abundance than the number of plants. Productivity is possibly a better indication of the 'importance' of a species in the community, or maybe Hurlbert's (1971) suggestion of using the change in production that would occur on removal of the species. Clearly these are less easy to measure than numbers of individuals.

1.1 iv) Grouping into categories other than species

We may wish to consider types other than species, for example, lumping together all insect-eaters, all herbivores, etc; or maybe in a different context we might wish to consider males and females as separate 'species'. As an example of the first, Horwitz (1978) considers the diversity of fishes classed into feeding groups. However, the kind of grouping does not affect the method of measurement and I shall continue to refer only to 'species' and 'abundance'.

1.1 v) The community

It is impossible to consider all the organisms - plants, bacteria, insects, mammals etc. - that occupy the area to be studied, so any study has to be restricted. For example, published papers have

considered the diversity of the plants alone of the area (Bazzas, 1968), the fish species of a lake (Barbour & Brown, 1974), and the reptiles and amphibians of a rain-forest (Lloyd, Inger & King, 1968). Thus the 'community' actually studied may not be a community in the usual biological meaning of the word since it may consist of several non-interacting, possibly incomplete food chains.

1.2 The information indices of diversity

1.2 i) Desirable properties for a diversity index

A useful source of diversity should include some information about the abundance of the species. Pielou (1975) lists the three following desirable properties for such an index H_S (a function of the relative abundances p_i of the S species in the community).

1. For any given S , H_S should have its maximum value when all the species are represented by the same number of individuals.
2. $H_{S+1} > H_S$ whenever all abundances in the community are equal. (Diversity increases with the number of species).
3. When a community is to be classified in more than one way, e.g. by species and genus, or by species and growth form,

$$H(A B) = H(A) + H_A(B)$$

i.e. the diversity under the double classification should equal the diversity under the A classification only plus the mean of the diversities under the B classification within the A groups. One would regard a community as being more diverse if its species belonged to many different genera than if they belonged to just one genus, or if its species exhibited a greater variety of growth forms. (For an example of this use of diversity measurement, see Lloyd, Inger & King, 1968).

1.2 ii) Shannon's index of diversity

Many indices can be found which satisfy the first two conditions. Khinchin (1957) showed that the only continuous function of the p_i to satisfy conditions 1), 3) and 4):-

4) Including an extra species represented by no individuals does not alter the diversity:

$$H(p_1, p_2, p_3, \dots, p_s) = H(p_1, p_2, p_3, \dots, p_s, 0)$$

is

$$H(p_1, p_2, p_3, \dots, p_s) = -\lambda \sum_{i=1}^s p_i \log p_i \quad (1.1)$$

where $\lambda > 0$

Any function satisfying conditions 1) and 4) also satisfies condition 2).

Setting $\lambda=1$ in (1.1) we have Shannon's index of diversity

$$H' = -\sum_{i=1}^s p_i \log p_i \quad (1.2)$$

Unfortunately, Shannon's index is not easy to calculate.

The maximum likelihood estimator of p_i is $p_i^* = N_i^*/N^*$ where N_i^* is the number of individuals of species i in the sample, and N^* is the total number of individuals in the sample.

However, the estimator of H' :

$$\hat{H}' = -\sum_{i=1}^s p_i^* \log p_i^* \quad (1.3)$$

is biased. The bias may be allowed for if we know S , the number of species in the population, (Basharin, 1959). In some cases we may be fairly sure that we know S , for example, if the community studied is the plants in an area of grassland in Britain, but often our observed value of S^* (the number of species in the sample) is no more than a lower bound for S . Secondly, use of (1.3) assumes that the individuals are a

random sample of the population, but this can be difficult to ensure. For example, if the method of sampling is a suction trap, and the insects are active for different lengths of time, then their probability of being caught is a function of their period of activity as well as of their abundance in the community. Pielou (1975) gives a method for calculating H' when S is not known.

Shannon's index should be used only for 'indefinitely large' communities from which examples may be removed without causing any perceptible change in the community. For a community in which all the individuals have been captured and identified, Brillouin's index, (which also satisfies Pielou's three conditions (1.2 i)) is appropriate.

1.2 iii) Brillouin's index of diversity

Brillouin's index H is given by

$$H = \frac{1}{N} \log \frac{N!}{\prod_{i=1}^s N_i!} \quad (1.4)$$

where N_i is the abundance of the i^{th} species and N is the total abundance of the community. Since H has been calculated from a completely censused community, it is free from sampling error and gives the true value for that community at that particular time.

For a sampled community, N and N_i are unknown, so Shannon's index must be used.

1.2 iv) Relationships between Shannon's and Brillouin's diversity indices

In information theory, Brillouin's index is used to measure the information content per symbol of a message and Shannon's index to measure the information content per symbol of a code (from which indefinitely many messages may be removed without

altering the code itself). But these analogies, although appealing, should not be taken too seriously. However, given a finite S -species community of N individuals in which all the individuals have been identified, with N_i individuals of species i , and an infinite community with proportion p_i individuals of species i , then

$H'_\infty > H'_S$ (Pielou, 1975). And using the approximation $\ln(n!) = n(\ln(n) - 1)$ (valid for very large values only of n , and no use for practical purposes):

$$\lim_{\min(N_i) \rightarrow \infty} H = H' \quad (\text{Pielou, 1975})$$

So if we take a sample from a large community and calculate Brillouin's index, the result is smaller than the value of Shannon's index for that community and theoretically tends to Shannon's index for very large samples.

1.3 Other diversity indices

1.3i) Simpson's Index

Simpson's index (1949) is defined as

$$\lambda = \sum_{i=1}^S p_i^2 \quad (1.5)$$

(with unbiased estimator

$$\hat{\lambda} = \sum_{i=1}^S \frac{N_i^* (N_i^* - 1)}{N^* (N^* - 1)} \quad (1.6)$$

It can be interpreted as the probability of two randomly chosen individuals belonging to the same species, or as the expected probability of a randomly chosen individual belonging to a given species. It decreases with increasing diversity; therefore $1 - \lambda$ or $1/\lambda$ have been used instead, (see, for example, Root, 1973; Rotenberry, 1978).

1.3ii) Probability of interspecific encounter

Hurlbert (1971) suggests various indices based on the encounters of an individual in the community, the basic index being his PIE or

'probability of interspecific encounter':- the proportion of random encounters between two individuals of the community that are between individuals of different species.

$$\begin{aligned}
 PIE &= \sum_{i=1}^S \left(\frac{N_i}{N} \right) \left(\frac{N - N_i}{N - 1} \right) \\
 &= \frac{N}{N-1} (1 - \lambda)
 \end{aligned}
 \tag{1.7}$$

Hurlbert's reasoning is that in a community with high PIE, the searching behaviour for mates or prey of the individuals in the community must be less random than could be acceptable with lower PIE.

1.3 iii) Good's family of diversity indices

Good (1953) proposed

$$H_{i,j} = \sum_{\ell=1}^S p_{\ell}^i (-\ln p_{\ell})^j \tag{1.8}$$

as a class of diversity measures. In this notation:

$$\begin{aligned}
 H_{0,0} &= S \\
 H_{1,1} &= \sum_{\ell=1}^S p_{\ell} (-\ln p_{\ell}) && \text{i.e. Shannon's index} \\
 H_{2,0} &= \sum_{\ell=1}^S p_{\ell}^2 && \text{i.e. Simpson's index}
 \end{aligned}$$

But there is little point in inventing a class of diversity measures unless the class parameters have a reasonable interpretation in a biological context.

1.3 iv) Hill's family of diversity indices

Good's parameters are apparently without biological meaning, but Hill (1974) introduces a family of diversity indices N_{α} where the class parameter α does have an interpretation:

$$N_{\alpha} = \left(\sum_{i=1}^S \omega_i p_i^{\alpha-1} / \sum_{i=1}^S \omega_i \right)^{\frac{-1}{\alpha-1}} \quad \text{with } \omega_i = p_i \quad (1.9)$$

Then $N_{-\infty}$ = the reciprocal of the proportional abundance of the rarest species

$$N_0 = S$$

$$\begin{aligned} \text{Define } N_1 &= \lim_{\alpha \rightarrow 1} (N_{\alpha}) \\ &= e^{H'} \end{aligned}$$

$$N_2 = 1/\lambda$$

N_{∞} = the reciprocal of the proportional abundance of the commonest species

Thus as α varies from $-\infty$ to ∞ the N_{α} come to depend less on the rare species and more on the common ones.

Note that $\log(N_{\alpha}) = -\frac{1}{\alpha-1} \log\left(\sum_{i=1}^S p_i^{\alpha}\right)$ which in information theory is the entropy of order α of a code.

1.3 v) Patil and Taillie's family of indices

Patil and Taillie (1977, 1979) suggest the family

$$\Delta_{\beta} = \left(1 - \sum_{i=1}^S p_i^{\beta+1}\right) / \beta \quad (1.10)$$

Δ_{β} is the average rarity of a species, where the rarity $R(p_i)$ of the i^{th} species is given by

$$R(p_i) = (1 - p_i^{\beta}) / \beta \quad (1.11)$$

and

$$\Delta_{\beta} = \sum_{i=1}^S p_i R(p_i) \quad (1.12)$$

The special cases are $\Delta_{-1} = S-1$, $\Delta_0 = \lim_{\beta \rightarrow 0} \Delta_{\beta} = H'$ and $\Delta_1 = 1-\lambda$. Suppose an observer of the community first encounters an individual of species i . The rarity function for Δ_{-1} is $(1/p_i - 1)$ which is the expected number of individuals further encountered before encountering again one of species i . The rarity function for Δ_1

is $(1-p_i)$ which is the probability that the second individual encountered is not of species i .

1.3 vi) Geometrical representations of diversity

If a community with S species having abundances N_1, N_2, \dots, N_S is represented in S dimensions by a point $P = (N_1, N_2, \dots, N_S)$ then the simplest measure of diversity is the distance of P from the origin :

$$d_M = \sqrt{\sum_{i=1}^S N_i^2} \quad (1.13)$$

This was suggested by McIntosh (1967)

Clearly this index increases with the number of individuals in the community. It is better instead to represent the community by $P' = (p_1, p_2, \dots, p_S)$, when the distance of the point representing the community from the origin is:

$$d' = \left(\sum_{i=1}^S p_i^2 \right)^{1/2} = \sqrt{\lambda} \quad (\text{see Fig. 1.1}) \quad (1.14)$$

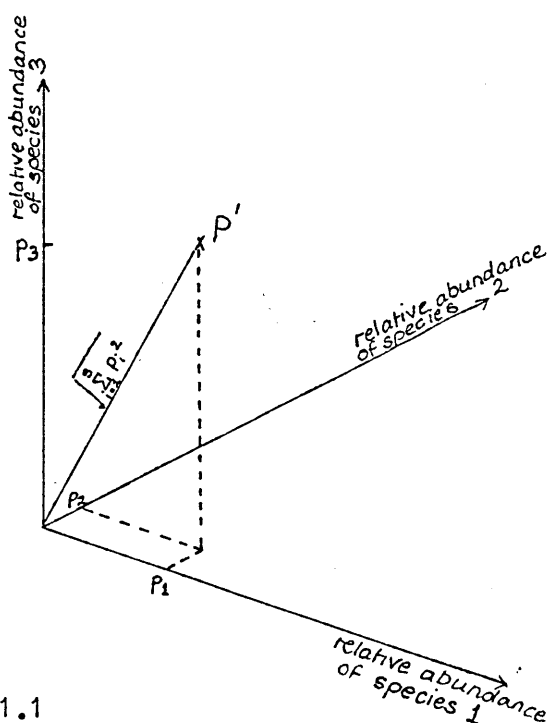


Fig. 1.1

P represents the community with relative abundances p_1, p_2, p_3 .

Since $\sum_{i=1}^S p_i = 1$ an obvious approach is as follows: if we represent a community with proportional abundances (p_1, p_2, \dots, p_S) by a point P on a simplex with S vertices such that the perpendicular distance of P from the face opposite the vertex A_r is p_r (see Fig. 1.2)

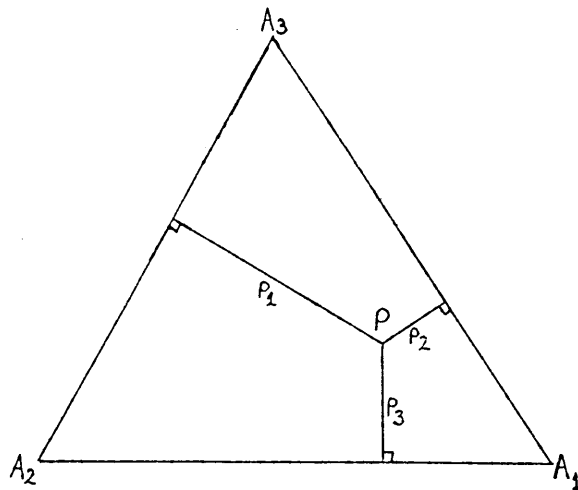


Fig. 1.2 The community with relative abundances p_1, p_2, p_3 represented on a simplex with 3 vertices.

then the distance² between the point P and the centroid is:

$$r^2 = \left(\frac{S-1}{S} \right) \left(\sum_{i=1}^S p_i^2 - \frac{1}{S} \right) \quad (1.15)$$

and the distance between the centroid and any vertex (which represents the minimum possible diversity on S species) is

$$r_{\max} = \frac{S-1}{S}$$

A possible index of diversity is

$$D^2 = 1 - \frac{r^2}{r_{\max}^2} = \left(\frac{S}{S-1} \right) \left(1 - \sum_{i=1}^S p_i^2 \right) \quad (1.16)$$

Simpson's index in this notation is given by

$$\frac{r^2}{r_{\max}^2} = \frac{S\lambda - 1}{S - 1} \quad (1.17)$$

1.4 Species abundance models

1.4 i) Introduction

An alternative approach is to fit a theoretical distribution to the observed distribution of abundances. We may then compare these curves for different samples, or use a suitable function of the parameters of the curves as a measure of diversity.

Many such approaches have been made. Some of the distributions are purely statistical, others, for example MacArthur's resource-apportioning 'broken stick' model, have been based on ecological models. I shall describe the two earliest approaches to fitting theoretical distributions.

1.4 ii) Log-series model

One of the earliest attempts to consider the distribution of species abundances is that of Fisher (Fisher, Corbet & Williams, 1943) who derives the log-series model as a limiting form of the negative binomial distribution which had already proved useful in describing the distribution of objects occurring in clumps.

Suppose the number of individuals of the j^{th} species in a population to be sampled is λ_j , and that the λ_j have distribution $f(\lambda_j)$. The probability that the j^{th} species will be represented in the sample by r members is given by the Poisson distribution

$$p_r^{(j)} = \frac{\lambda_j^r e^{-\lambda_j}}{r!} \quad (1.18)$$

The probability p_r that any species will be represented in the sample by exactly r members is

$$p_r = \int_0^\infty \frac{\lambda^r e^{-\lambda}}{r!} f(\lambda) d\lambda \quad (1.19)$$

If λ has a gamma distribution

$$f(\lambda) = \frac{\left(\frac{m}{k}\right)^{-k} \lambda^{k-1} e^{-\lambda k/m}}{\Gamma(k)} \quad (1.20)$$

then p_r has a negative binomial distribution

$$p_r = \frac{\Gamma(k+r)}{r! \Gamma(k)} \left(\frac{m}{k}\right)^r \left(1 + \frac{m}{k}\right)^{-(k+r)} \quad (1.21)$$

The parameter m depends on the proportion of the population sampled, and k is a measure of the variation of the λ_j .

Fisher observed that natural communities have a high degree of heterogeneity in their species abundances and so k tends to be small. So he considered the effect of letting k tend to zero in (1.21). If we put $\frac{m}{k} = \frac{x}{1-x}$ and collect terms independent of r into a single constant C , then

$$p_r = C \frac{\Gamma(k+r)}{r!} x^r \quad (1.22)$$

Then $\lim_{k \rightarrow 0} p_r = \pi_r$ say, is given by

$$\begin{aligned} \pi_r &= \lim_{k \rightarrow 0} C \frac{\Gamma(k+r)}{r!} x^r \\ &= \frac{x^r}{r!} \lim_{k \rightarrow 0} C \\ &= \alpha \frac{x^r}{r!} \end{aligned}$$

But $k=0$ is not a possible parameter value for the gamma distribution, so the form of the gamma distribution for very small k is of interest. Kempton & Taylor (1974) plot the likelihood surface for the parameters S (the expected number of species in the population) and k for the negative binomial distribution, and show that the position of maximum likelihood is exceedingly ill-defined, supporting Fisher's suggestion

of letting k tend to zero. Kempton obtains the limiting form for small k as follows: note that the probabilities p_r in (1.21) may be expressed as

$$p_0 = 1 + k \log(1-x) + o(k)$$

$$p_r = \frac{kx^r}{r} \left(1 + k \log(1-x) + o(k) \right) \quad r = 1, 2, \dots$$

where $x = m/(m+k)$

Hence if k is small and pk not too large (i.e. a small proportion only of each species in the population has been sampled) the expected values from the negative binomial model will be well approximated by

$$E_r = kS \frac{x^r}{r} \quad (1.23)$$

$$= \alpha \frac{x^r}{r}$$

Now, x depends on m and is therefore a function of sample size, whereas α depends on k and S and is truly a population parameter. It depends on the number of species in the population and (through k) on the heterogeneity of their abundances, and in fact for large samples, if the size of the sample is multiplied by e , the expected number of species in the sample is increased by α . So α can be used as a measure of diversity. As α is independent of sample size, so the expected value of α in any sample is the same as the population value, and we can use α to compare samples of different sizes.

1.4 iii) Lognormal distribution

The next approach is that of Preston (1948) who observed that if a plot is made of the number of species against \log (to base 2) of species abundance, the resulting curve is often well-fitted by a normal distribution (i.e. the distribution of species abundances is log-normal) - truncated however by a 'veil-line' (Preston's term) because of the impossibility of a species being represented by less

than one whole individual (see Fig. 1.3). As the sample size increases, more rare species are represented in the sample,

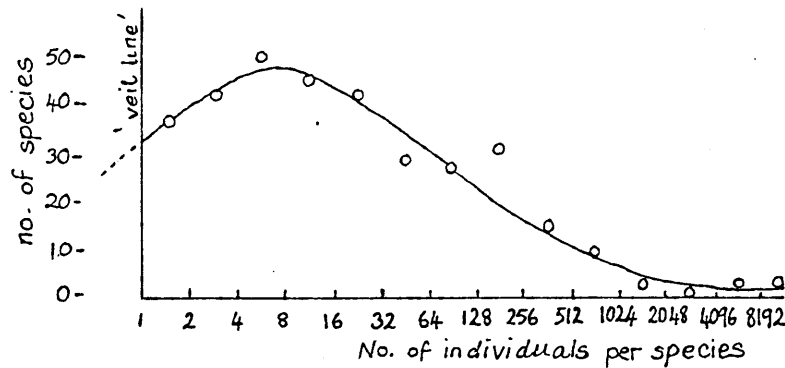


Fig. 1.3

Fitted log-normal distribution (redrawn from Preston, 1948)

and less of the curve is truncated. Preston suggests that doubling of the sample size will lead to doubling of the expectations of all the species abundances, which is equivalent to shifting the whole curve one interval to the right and withdrawing one more class from 'behind the veil'. A function of S and the standard deviation σ , for example S/σ (Kempton & Taylor, 1974) can be used as a measure of diversity.

1.4 iv) Broken stick model

Attempts have been made to justify the log-normal distribution on purely ecological grounds (for example May, 1975) as the pattern of abundances resulting from the interplay of many more-or-less independent factors. However one or two models have been conceived entirely from ecological considerations. The most important is the broken stick model of MacArthur (1957). The available resources are considered as a stick to be divided by random breaks among the

species present, whose relative abundances will be equal to the proportion of the resource stick allocated to them. The abundance of the i^{th} most common species (the length of the i^{th} longest segment) is

$$E(y_i) = \frac{1}{S} \sum_{x=i}^S \frac{1}{x} \quad (1.24)$$

1.5 Index based on the quartiles of the distribution

The disadvantage of fitting a model is that different communities are difficult to compare unless fitted distributions have been summarised in the form of a diversity index. Even then, it is difficult to compare an index value derived, for example, from the log-series model with a value of a different index from a population better fitted by the log-normal model. Kempton & Taylor (1976) regard the fitting of a model as a means of smoothing the data prior to calculating a diversity index. They argue that in this case it is preferable to fit the same model to each data set under consideration even if some of the data sets might be better fitted by another model. Kempton & Taylor find in their survey of moths that the abundance distribution of the 50% of species of intermediate abundance is more characteristic of a site and fluctuates less from year to year than the abundance distribution of all the species.

Therefore they define their quartile statistic Q to be the reciprocal of the slope of the cumulative log abundance curve of the 50% intermediate species: (see Fig. 1.4)

$$Q = \frac{1/2 S}{\log R_2 - \log R_1} \quad \text{where } R_1 \text{ and } R_2 \text{ are the quartiles} \quad (1.25)$$

thus ignoring the 25% most abundant species as being too much subject to fluctuation and the 25% rarest as being unimportant in terms of community structure. It has a simple theoretical expression when the species abundances are assumed to be distributed according to

the log-series or log-normal models. For the log-series model:

$$Q = \alpha \quad (1.26)$$

and for the log-normal model:

$$Q = \frac{cS^*}{\sigma} \quad (1.27)$$

where c depends on the proportion of species present in the sample. If $S^* = S$,
 $c = 0.371$

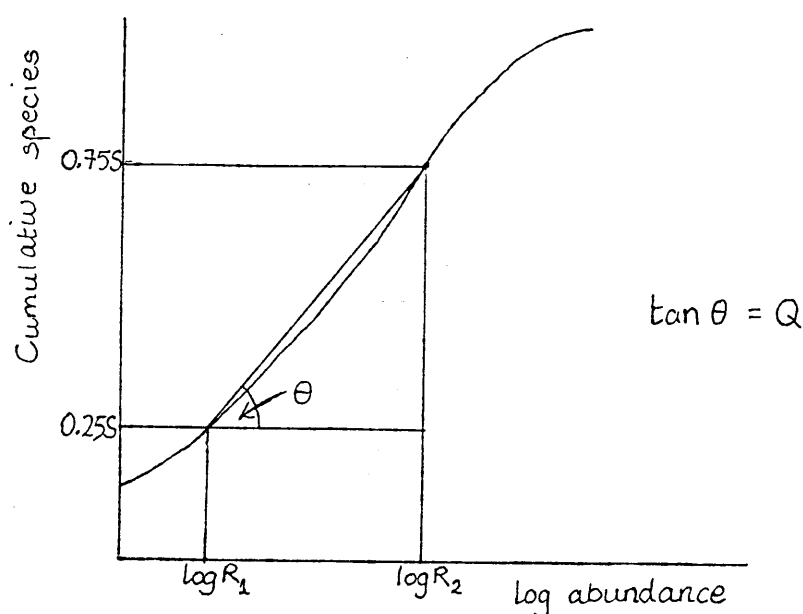


Fig. 1.4 Evaluation of Q from the cumulative species abundance curve. (Redrawn from Kempton & Taylor, 1976).

1.6 A partial diversity ordering

There is no guarantee that two apparently sensible measures of diversity will give the same ranking of communities by diversity. (Hurlbert, 1971, gives a highly unrealistic example. It is likely that this is not such a problem in practice). Patil & Taillie (1979) show how to define a partial ordering of communities using the concept of intrinsic diversity. Community B is described as being intrinsically more diverse than community A if it can be derived from A by a sequence of the two operations:

- i) introducing a new species to share the abundance of a species

already present.

- ii) transferring abundance between two species to make them more equivalent.

Equivalently, community B is intrinsically more diverse than community A if the plot of cumulative proportional species abundances against rank for A is everywhere above that for B. If the two curves intersect, then A and B are not comparable. [note that if B has more species than A, then either B is intrinsically more diverse, or the two are not comparable]. An intrinsic diversity function is one which orders communities according to their intrinsic diversity whenever such an ordering is possible. A necessary and sufficient condition for a function f to be an intrinsic diversity function is that it should be Schur-concave, (Kempton, 1979; Solomon, 1979) i.e.:

$$\left(\frac{\partial f}{\partial p_i} - \frac{\partial f}{\partial p_j} \right) (p_i - p_j) - 2 (p_i - p_j)^2 \leq 0 \quad \text{for all } p_i, p_j$$

The set of Schur-concave functions includes the indices of Simpson, Shannon, McIntosh, Lloyd & Ghelardi, and Brillouin; and Hill's measures N_α for $\alpha > 0$; thus these indices give a set of communities the same diversity ordering provided their curves of cumulative proportional abundance vs rank do not intersect.

1.7 Components of species diversity

1.7 i) Introduction

It is interesting to try to measure separately the components of diversity due to species richness (number of species) and the distribution of species abundances ('equitability' or 'evenness'). Use of a single index of diversity entails lumping together communities which have the same diversity but which may have

considerable differences in number of species and distribution of abundances. This seems undesirable. Secondly, the existence of a 'tail' of rare species has little effect on diversity indices such as Simpson's or Shannon's. Although the tail may not be important to the community now, the tail is the reservoir of species which may be able to increase should conditions alter, and so are important as regards the future of the community. Consideration of the species abundance curve tells of the existence of a tail, but often the fitting of a theoretical distribution to a species abundance curve is no more than a tool for finding a single diversity index such as the \log -series α . Consider the two communities A and B, both with 100 individuals, with species abundances as follows:

A:	28	20	15	12	8	6	4	3	2	2					
B:	40	20	10	7	5	4	3	2	2	2	1	1	1	1	1

Which is the more diverse? Simpson's index and Shannon's index suggest they have nearly equal diversities ($(1 - \lambda) = 0.83$ for A and 0.78 for B; $H' = 1.98$ for A and 1.95 for B). According to the ideas of section 1.6 they are not comparable since their cumulative ranked proportional abundance curves intersect. But two things are immediately obvious: B has 15 species whereas A has only 10, and the abundances of community B are less evenly distributed than those of community A. And so we can see the usefulness of measuring separately these two aspects of diversity.

1.7 ii) Existing measures of equitability

Species richness is a measure of the mean of the distribution of abundances (mean proportional abundance = $(\sum_{i=1}^S p_i)/S = 1/S$).

Normally we would use variance as a second descriptive parameter for a distribution, but in this case variance $\left(\left[\sum_{i=1}^S (p_i - 1/S)^2 \right] / (S-1) \right) = \left(\sum_{i=1}^S p_i^2 - 1/S^2 \right) / (S-1)$ is by the nature of the observed distributions heavily dependent on the mean. We need some index of equitability that is independent of the number of species in the community. The most obvious way is to compare the observed diversity with the maximum value possible for that number of species, e.g.

$$J' = \frac{H'}{H'_{\max}} = \frac{H'}{\log S} \quad (1.28)$$

$$= - \sum_{i=1}^S p_i \log_S p_i$$

or the index r^2/r_{\max}^2 considered in section 1.3 vi). Another way is to calculate the ratio of the observed number of species to the expected number of species required to give the same diversity value for a distribution such as the broken stick model, (section 1.4 iv) which is more equitable than most natural communities (see Lloyd & Ghelardi, 1964).

For his family of diversity indices (introduced in section 1.3 iv) Hill observed that as α varies from $-\infty$ to ∞ , N_α comes to depend more and more on the common species and less and less on the rare. So we may consider

$$E_{a,b} = N_a / N_b$$

as a continuum of evenness measures; for example, Buzas and Gibson (1969) used $E_{1,0} = e^{H'}/S$

1.7 iii) A criterion for equal equitability

Before we can decide whether a suggested measure of equitability is in fact independent of the number of species in the collection,

we have to define what we mean by equal equitability in communities with different numbers of species. Consider the two communities of section (1.7i). A plot of log. %age abundance vs species rank for both communities is shown in fig. 1.5. The plot for community A (fig. 1.5a) is very nearly a straight line, whereas that for B (fig. 1.5b) has a definite 'sag' in it. The lesser equitability of B shows up even more clearly when both graphs are standardised to the same length of the species rank axis (fig. 1.5c).

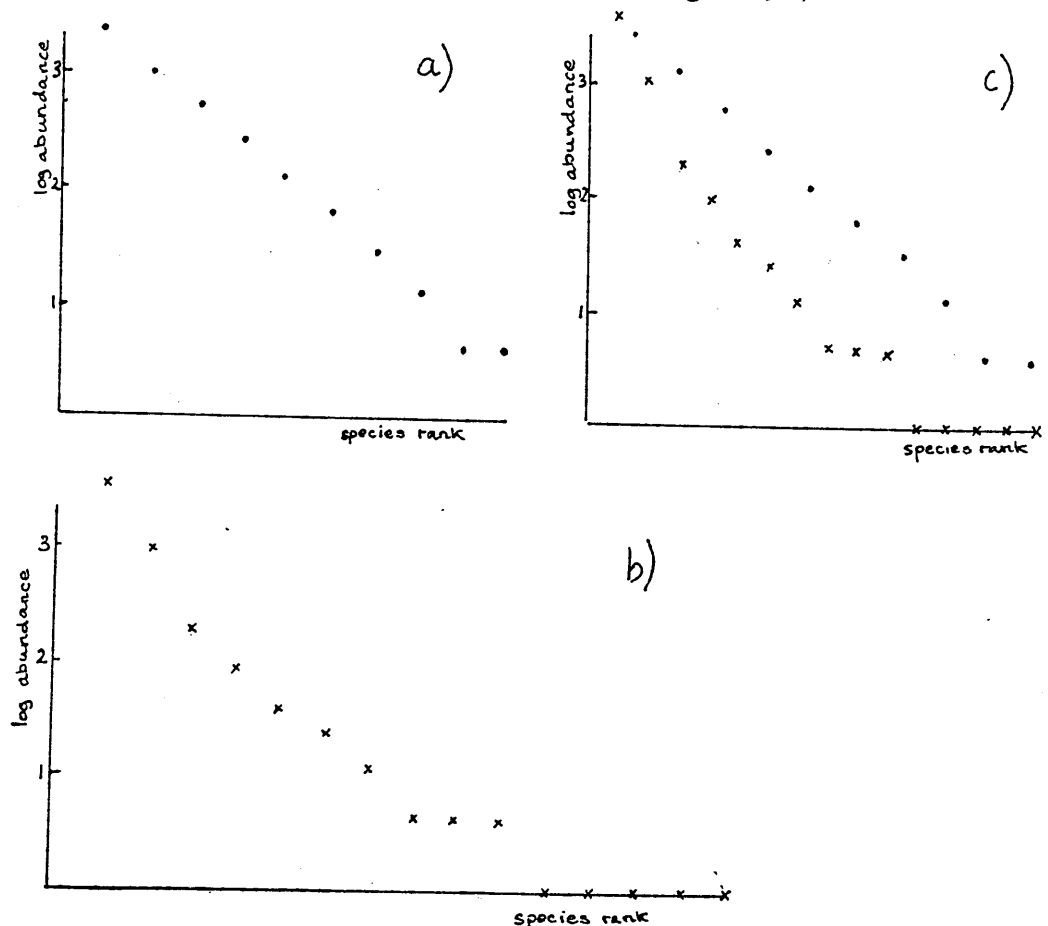


Fig. 1.5 Log. abundance vs species rank for the two communities of section 1.7i).

This suggests that we may state a criterion of equal equitability:
Two communities have the same equitability if their ranked log. proportional species abundance curves are identical when rescaled to equal length on the species rank axis.

1.7 iv) Practical test criteria for equal equitability

However it is impossible to test a proposed equitability index on the infinity of possible curves that could arise. We must be content with a few special cases.

1.7 v) Hill's criterion

Hill (1975) gives the following criterion for an index of equitability: suppose there are two communities A and B, each with N individuals. Community A has 2S species in proportions $p_1, p_1, p_2, p_2, p_3, p_3, \dots, p_s, p_s$ and community B has S species in proportions $2p_1, 2p_2, 2p_3, \dots, 2p_s$; then A and B should have the same equitability. All Hill's measures $E_{a,b}$ satisfy this criterion though $H'/\log S$ does not.

1.7 vi) Hurlbert's criterion

Hurlbert (1971) considers that two communities are equally equitable if both have every species but one represented by a single individual. However, consideration of the rather absurd case - community A: 100 species, abundances 2,1,1,...,1; community B: 2 species, abundances 100,1 - is sufficient to cast doubt on the appropriateness of this criterion.

1.7 vii) 'Model' criterion

It seems reasonable to assume that communities with different numbers of species whose abundances are generated by the same model with the same parameters should have the same equitability.

According to this criterion, and using abundances generated by the broken stick model, $e^{H'}/S$ and $1/\lambda e^{H'}$ (both of which satisfy Hill's criterion) perform rather badly, varying considerably with the number of species (see Fig. 1.6). The best index according to this criterion seems to be $H'/\log S$, which is in fact the most widely used. (See Sheldon, 1969)

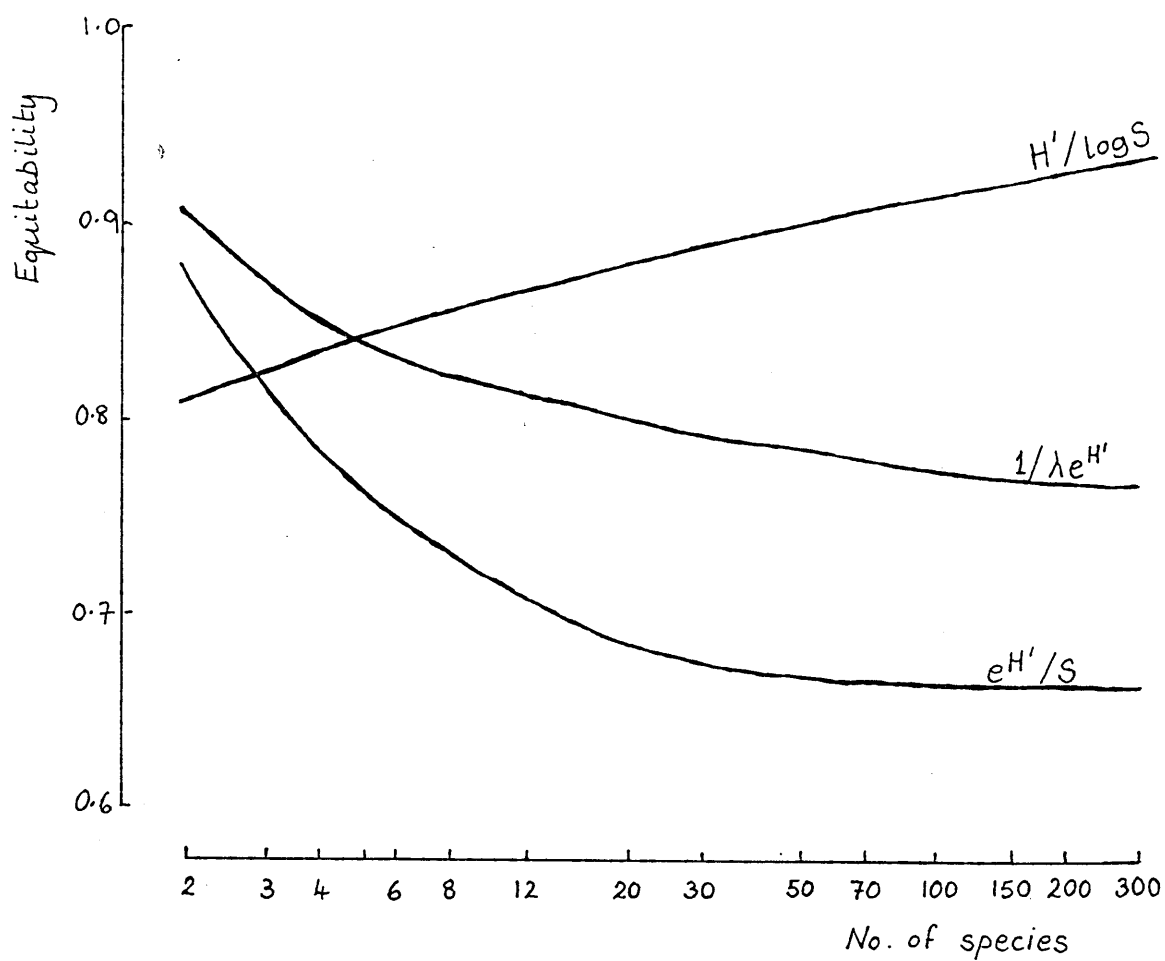


Fig. 1.6

Relationship of three equitability indices to number of species.

Species abundances given by broken stick model.

1.7 viii) Equitability orderings

It is not enough to decide whether two communities are equally equitable: we need also to be able to decide whether one community is more or less equitable than another. Therefore we must consider the conditions to be satisfied by an equitability measure \mathcal{E}_S which gives a value for equitability to a community with S species.

1.7 ix) Maximum equitability

The equitability measure should take its maximum value when all the p_i are equal.

If \mathcal{E}_S is to be independent of S , then the maximum value $\mathcal{E}_S^{(max)}$ should also be independent of S . Hill's measures $E_{a,b}$ and $H'/\log S$ by definition satisfy this rather trivial condition, but Lloyd & Ghelardi's index (section 1.7 ii) does not.

1.7 x) Minimum equitability

A suitable choice for the condition of minimum equitability is the case $p_i \rightarrow 1$ and $p_j \rightarrow 0$ for all $j \neq i$.

1.7 xi) Continuity (Engen, 1979)

Consider the community with proportional abundances

$$p_i = \frac{1}{S-1} - \delta \quad i = 1, 2, \dots, S-1$$

$$p_S = \delta$$

As $\delta \rightarrow 0$ the community approaches the $(S-1)$ species community of maximum equitability and, it may be argued, should have an equitability value close to $\mathcal{E}_{S-1}^{(max)}$, which, in section 1.7 ix), we argued should be equal to $\mathcal{E}_S^{(max)}$; which in turn suggests that \mathcal{E}_S in this example is not a monotonic function of δ . So the conditions of sections 1.7 ix) and 1.7 xi) appear incompatible.

1.7 xii) A partial equitability ordering

Taillie (1979) considers the Lorentz curve, cumulative proportion of species vs cumulative proportion of individuals, and suggests that

a proposed equitability function \mathcal{E} is consistent with the Lorentz ordering if $\mathcal{E}(P) \geq \mathcal{E}(Q)$ whenever the Lorentz curve of community P is everywhere above that for Q. Two communities with equal equitability according to sections 1.7 iii) and 1.7 v) have equal equitability under the Lorentz ordering.

Taillie further suggests that \mathcal{E} should be consistent with intrinsic diversity for communities having the same number of species, which is necessarily true for an index satisfying the Lorentz ordering. Hill's indices $E_{a,b}$ satisfy these conditions for $b = 0$.

1.8 Discussion

1.8 i) Introduction

Neither diversity nor equitability have an obvious interpretation that will allow us to define a way of measuring them that is accepted without argument by all. Therefore a large number of approaches have been tried, emphasising different aspects of the way the individuals have been divided up into different species.

1.8 ii) The effect of sample size on the number of species in the sample

The number of species in the sample is dependent on the size of the sample, as are most of the indices considered above. We wish to compare the diversities of different communities from which the samples will have different sizes, so we need to overcome this problem. One attempt is the rarefaction index of Sanders (1968). Using this method, for each community the expected number of species at a range of smaller sample sizes is calculated, assuming that the species occur in the same proportions as in the original sample. The expected values for different communities at each sample size may then be

compared. However, Sanders' method does not give a true estimate of the expected number of species.

The number of individuals of a particular species actually drawn in a smaller sample is subject to fluctuation, and by not taking this random element into account, Sanders' method overestimates the number of species in the smaller sample. Simberloff (1972) has shown by repeated sampling from Sanders' own sample of 1002 individuals that the method does indeed overestimate the number of species present. More importantly, Fager (1972) shows that this overestimation is a function both of the average number of individuals per species and of the distribution of individuals among species (for an extremely equitable distribution the error may be as much as 50%, (Hurlbert, 1971)) and so bias cannot be expected to 'cancel out' between communities.

Simberloff's solution was to use computer simulation of the drawing of m individuals from the large sample at random without replacement. But this is unnecessary since the expected number of species in the smaller sample is given by the hypergeometric distribution:

$$E(S_m^*) = \sum_{i=1}^{S^*} \left[1 - \frac{\binom{N^* - N_i^*}{m}}{\binom{N^*}{m}} \right] \quad (1.29)$$

(Hurlbert, 1971)

The properties of these expected values are considered by Smith & Grassle (1977). Thus using the hypergeometric distribution to generate the expected number of species present at each sample size we can use the idea of rarefaction to compare samples of different sizes.

1.8 iii) The effect of sample size on diversity indices

The rarefaction method is of no use when we are looking for a diversity index using the abundances of the species present. Fortunately, provided the samples are large enough, the values of both Shannon's index and Simpson's index level out and do not increase further with sample size. The same is true of Hurlbert's PIE.

The diversity α from the log-series model is theoretically independent of sample size and in practice its dependence on sample size seems to be slight, and is a suitable parameter when the samples are well fitted by the logseries curve.

1.8 iv) Biological interpretations of diversity

I feel that the search for a truly biological definition of diversity can mislead. The biologically inspired models such as the broken stick give distributions of abundance that are more equitable than almost all natural communities (with a few exceptions, see Schlesinger, 1978). Simpson's index gives the probability that two individuals drawn at random will be of the same species; but in natural communities the individuals of different species are unlikely to be randomly mixed, and so this interpretation of Simpson's index does not tell us whether it is in practice a useful index. Hurlbert explains his PIE as an indication of how successful purely random mate-searching or prey-searching is likely to be, but again this assumes that the species are randomly mixed in the community.

1.8 v) Theoretical distributions

The approach of fitting a theoretical model to the distribution of species abundances seems promising, although it is difficult to

compare curves, and it is best to consider the fitting of a theoretical distribution as a way of smoothing the data prior to calculating an index. We need make no attempt to justify the parameters derived from such a model on biological grounds. But the log-series and log-normal models are limited in their applicability - not by a long way is every observed distribution of species abundances well fitted by one of these theoretical distributions, and we cannot attempt to measure diversity using the parameters of a model that does not fit the data - and so a good index to use appears to be Kempton's Q-statistic.

1.8 vi) Choice of a single index of diversity

Instead of looking for biological meanings to an index of diversity, we should judge it according to simple criteria, such as conditions 1), 4), and 2) of section 1.2 i). The index should increase as more species are added to the community, should not change if a new species with no representatives in the community is included in the calculation, and should have its maximum value when all the species are equally represented. Condition 3) seems to me an irrelevant luxury - very rarely in practice is diversity measured on more than one level.

There are many indices satisfying 1), 2) and 4); and which one to use seems a matter of personal choice depending on the particular characteristics of each. For example Simpson's index has a simpler unbiased estimator than Shannon's, but Simpson's index is less sensitive than Shannon's to all but the commonest species.

Simpson's index and Shannon's index are both more affected by common species than by species of intermediate or low abundance. If this is felt to be undesirable, parameters of the log-series or log-normal models may be used instead, but only if these give an adequate

fit to the data. An alternative is the quartile statistic which uses the middle range of abundances only.

Discrimination between sites is likely to be an important factor. Kempton & Taylor (1974) have found that the α parameter of the log-series model gives better discrimination than S & σ of the log-normal model, either separately or combined into a single function.

1.8 vii) Measures of equitability

I feel Taillie's approach is the nearest to a working definition of equitability but it defines only a partial ordering. Perhaps this is as far as we can go.

1.8 viii) The effect of sample size on equitability

Clearly, for small samples, both the number of species and their estimated abundances will change with increasing sample size. When the sample size is large enough for the proportional abundances of all but the rarest species to be reasonably well estimated, the diversity, as measured by an index such as Shannon's or Simpson's, will change very little. But the number of species in the sample will continue to increase with the occasional capture of a previously unrepresented species. The addition of these very small proportional abundances means that the distribution of abundances becomes more inequitable, and so 'equitability' continues forever to decrease. More clearly, any index of equitability based on a ratio of 'diversity' to number of species must continue to decrease since 'diversity' is constant and number of species is increasing. I know of no way to compare the equitability of two samples of different sizes.

1.9 Summary

To summarise, the main problem in measuring diversity seems to me to be as follows: since we have no concrete, measurable idea of what diversity or equitability is, we have to in effect work backwards, choosing a likely-looking measure, seeing whether it fits in with our rather indefinite ideas in some simple cases which are unlikely to be encountered in practice (such as when all the species are equally abundant, or when all the communities have the same number of species - see Pielou's conditions for a diversity index), and if it does, we say we have measured diversity. Such a procedure is unlikely to produce unanimity on the subject. The closest approach to defining diversity is the partial ordering discussed in section 1.7xii).

2 The relationship of diversity to the environment

2.1 Introduction

Many authors have tried to explain differences in diversity as the result of ecological and environmental factors; for example, Kullberg (1968) was interested in differences in diversity along a temperature gradient in a thermal spring, and Brown (1973) related the number of species of rodent in desert sand-dunes to ecological and biogeographic factors. On a larger scale there is an apparent general increase in diversity from high to low latitudes. A suggested explanation (e.g. Sanders, 1968) for these differences in diversity is that high diversity can only develop in the absence of severe environmental fluctuations.

2.2 Diversity as a result of environmental predictability

2.2 i) General theory

The theory that high diversity is the result of a stable and predictable environment has been stated and developed by many authors. One of the widely-quoted sources is Sanders' (1968) stability-time hypothesis. The theory suggests that, in an unpredictable environment, species abundances are regulated by physical factors (such as temperature and abundance of food). Only species adapted to life over a wide range of conditions will persist. Each species will be competing for a wide range of resources so few species will be able to coexist and diversity will be low. On the other hand, in a stable environment species abundances will be controlled by interaction with other species; in the absence of sudden fluctuations in the environment which reduce population numbers, competition between species becomes an important controlling factor. But a predictable supply of resources over a long enough period of time permits specialization as a way of avoiding competition, and in turn

specialization allows more species to coexist.

It may be suggested that speciation results from the existence of a wide variety of phenotypes in a population, which can occur only in a population subject to a wide range of different environmental pressures - see, for example, the discussion of Slobodkin and Sanders' (1969) paper. However, one can reason that unstable environments support less diverse communities by the extinction of all species except those able to live in variable conditions. Species unable to exist over a wide range of conditions will become extinct in variable environments but will find refuge in predictable environments. For a species to invade a predictable environment requires that the species should be able to compete successfully with those species already there; a species which is to survive in an unpredictable environment needs to 'compete' successfully with the environment as well.

2.2 ii) Diversity changes during ecological succession

A similar theory emerges from work on diversity and ecological succession. Only in a predictable environment can succession be expected to proceed to its climax, and in such an environment the expected sequence is this: during the early stages of invasion of a new territory, when there is little competition, colonization is by species adapted to fast growth and fast reproduction, and diversity increases with the rapid addition of new species. Later, as the territory becomes more crowded, so space and resources become relatively less abundant, competition between species becomes increasingly important and the number of species falls somewhat because only the species best adapted to competition survive (see, for example, MacArthur & Wilson, 1967).

2.2 iii) Predictions of mathematical models

Mathematical models support the idea that only predictable environments give rise to high diversity. May (1974a, 1974b) suggests that a model describing a more complex community has in the space of species interaction parameters a smaller region where it is stable than has a model describing a simple community, and therefore small fluctuations in parameters will send the system into a region of parameter space where it is unstable. (May's work will be discussed further in section 2.3 iii). Thus it is conceivable that only a predictable environment will allow the continued existence of a highly diverse community with many interactions. If a community is to be stable in an unpredictable environment, it will need to be stable over a wide range of parameter values, and according to the model it will need to be relatively simple, with few species.

2.2 iv) Experimental evidence indicating that high diversity is associated with environmental predictability

Evidence that high diversity is associated with environmental predictability is given by Rotenberry (1978) in his work on birds. Considering environmental variables, he used principal components analysis to define the position of his sites along a gradient which can be identified as running from mild environmentally stable sites to severe unstable sites. He calculated the diversity of bird species from the abundances at each of these sites, and found a significant decline in diversity from the predictable to the unpredictable sites.

Horwitz (1978) studied 14 American rivers (chosen for their freedom from large man-made obstacles such as dams) and related the number of fish species to the variability of the water flow (an obvious way in which the environment of a fish might vary). Those

rivers which had the highest headwater variability had the lowest headwater fish diversity (see Table 2.1), i.e. among the different rivers, the most predictable sites had the most species. In Table 2.1, thirteen of the rivers are ranked by headwater variability (1=most variable) and by numbers of species (1=fewest species). The two rankings are highly correlated (Spearman's rank correlation coefficient = 0.77).

	Rank of headwater variability	Rank of headwater species richness	Rank of slope of variability progression (1=greatest slope)	Rank of rate of species addition (1=higher addition no.)
A. Current River	1	1	1	1
B. Grand River	2	7.5	2	11
C. Blackwater River	3	4	3	6
D. Salt River	4	3	4	5
E. Kaskasia River	5	9	6	4
F. Gasconade River	6	2	7	2.5
G. Meramec River	7	6	5	2.5
H. Raccoon Creek	8	7.5	8	8
I. LaMoine River	9	5	9	12
J. Sandusky River	10	10.5	10	9
K. Kanakee River	11	10.5	11	10
L. Little Maine River	12	12	12	7
M. Mad River	13	13	13	13
N. Powder River	-	-	14	14

Table 2.1

Overall ranking of variability of flow and species richness for 14 rivers (from Horwitz, 1978).

The variability of water flow decreases downstream. The slope of the linear regression of variability on distance downstream (taking into account also the number of tributaries that have joined the river) can be used as a measure of the decrease in variability. Table 2.1 shows also how the rate of addition of new species as one moves downstream is significantly correlated with the degree of decrease in variability (Spearman's rank correlation coefficient = 0.65).

2.2 v) Evidence that specialization increases in predictable environments

Evidence exists suggesting that the greater number of species in a predictable environment is the result of specialization. Taylor & Taylor (1977) show that this is true for predatory gastropods, with more species in the tropics (a relatively predictable environment) than in the less predictable higher latitudes; and both specialist and generalist species are found in the tropics whereas only the generalist families are found at higher latitudes (see Fig. 2.1).

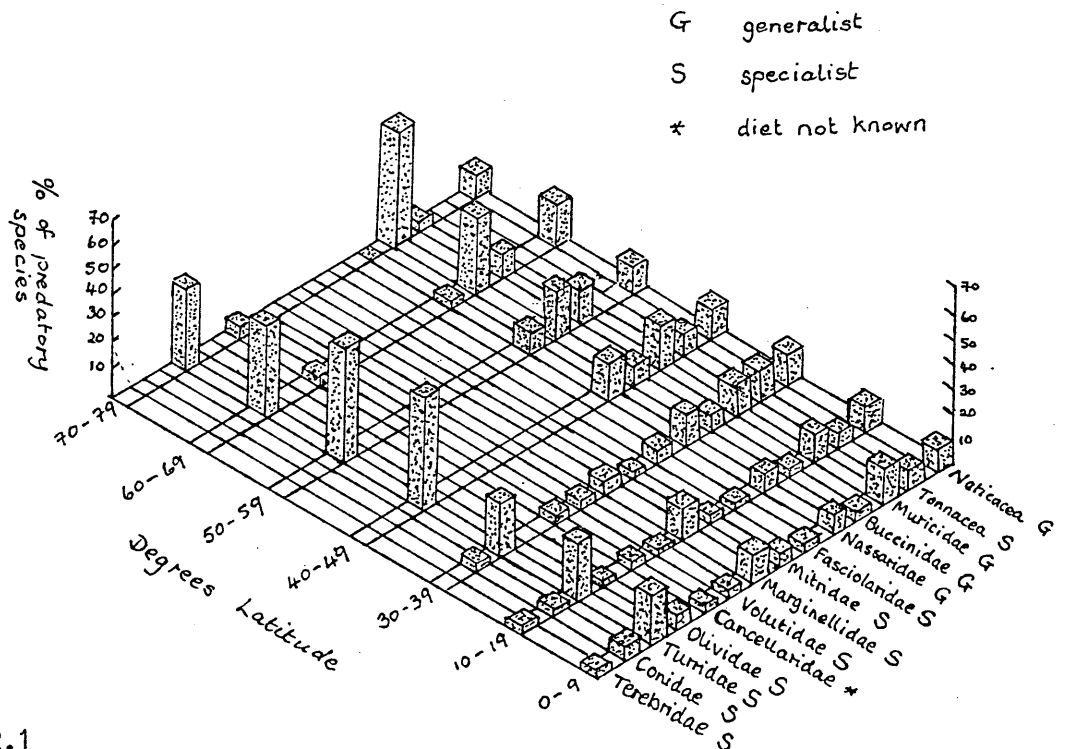


Fig. 2.1

Latitudinal variation in the composition of the predatory prosobranch fauna on the eastern Atlantic shelf (from Taylor & Taylor, 1977).

Similarly, Ostler & Harper (1978) find that animal-pollinated flowers are more abundant in diverse flowering plant communities, as are plants where access to nectar is restricted by morphological barriers, whereas wind-pollinated flowers are more abundant in less diverse flowering plant communities (see Fig. 2.2), i.e. specialization of fertilization (animal-pollinated flowers) is related to high diversity (i.e. unpredictability) of the floral environment.

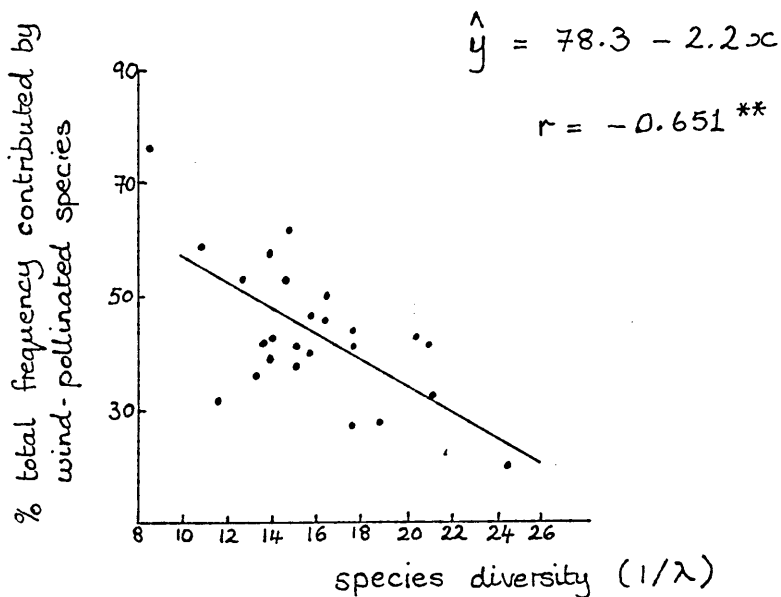


Fig. 2.2

The relationship between species diversity and the percent sum frequency contributed by wind-pollinated plant species in 25 Wasatch Mountain plant communities (from Ostler & Harper, 1978).

2.2 vi) Evidence that competition is important in predictable environments

It is suggested above that competition between species is the mechanism by which specialization occurs in predictable or favourable environments. In unpredictable and unfavourable environments, population

levels are depressed by sudden changes or general harshness of the environment, and the total abundance of each species is not sufficient for competition to be a regulatory factor. But if the environment is favourable and predictable, population levels increase until competition becomes important, and specialization is a means of reducing competitive pressures. Evidence that competition is indeed an important aspect of natural communities is given by Menge (1972) for starfish and by Kohn (1978) for the predatory gastropod Conus miliaris.

Menge was concerned with the competition between the two starfish Pisaster and Leptasterias. He removed all the Pisaster from one site and added 250 specimens to the original 55 specimens at another site. A third site was used as control. The mean size of Leptasterias increased significantly at the first site and decreased significantly at the second, while there was no change at the third (control) site. Similarly, the biomass per square metre of Leptasterias more than doubled at the first site and decreased at the second site, while at the control site there was an increase in biomass per square metre of Pisaster and a decrease in biomass per square metre of Leptasterias. Thus it seems that the growth of Leptasterias is restricted under natural conditions by competition with Pisaster.

Kohn investigated the feeding habits of Conus miliaris, the only Conus species occurring on Easter Island. He showed that its density was as great as that of all Conus species together elsewhere in the Indo-West Pacific, and that its diet was more varied, over half of its diet on Easter Island being of four species not eaten by Conus miliaris where other species of Conus co-occur.

Figure 2.3 shows the greater diversity (as measured by Shannon's index according to the method of Pielou, 1975) per number of prey items of the Conus miliaris diet on Easter Island compared with other Indo-West Pacific localities. A similar expansion of diet occurs in Conus californicus, the only Conus in its habitat in California.

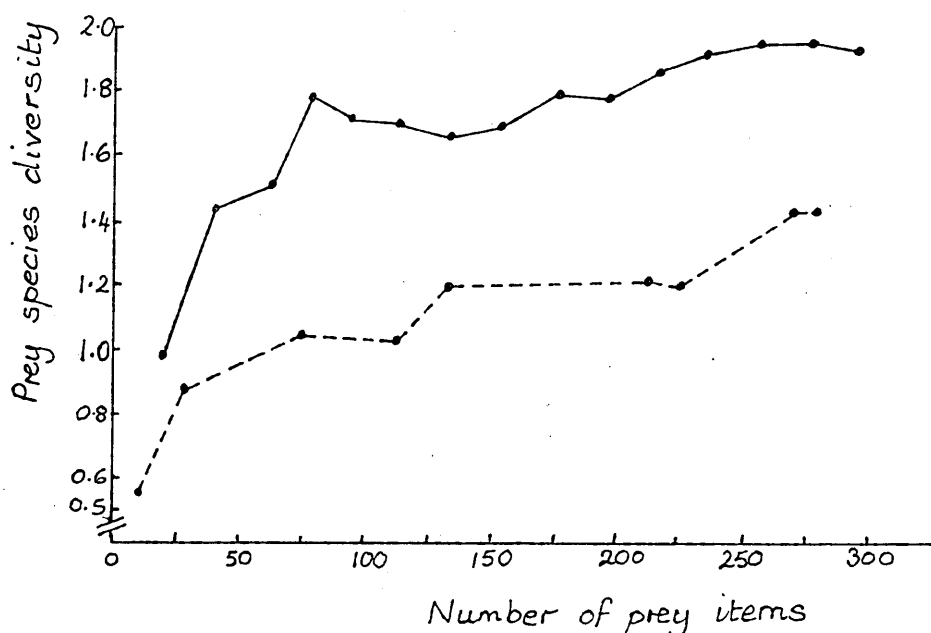


Fig. 2.3

Cumulative values of prey species diversity of Conus miliaris at Easter Island (solid line) and in central Indo-West Pacific localities combined (dashed line). (from Kohn, 1978).

Further evidence arises from the work on succession. Shafi & Yarranton (1973) investigated the diversity in the first stages of post-fire succession. They found some evidence of an increase followed by a levelling-off of diversity to a lower value in the

later stages, as expected from the theory presented in section 2.2 ii) (see Fig. 2.4).

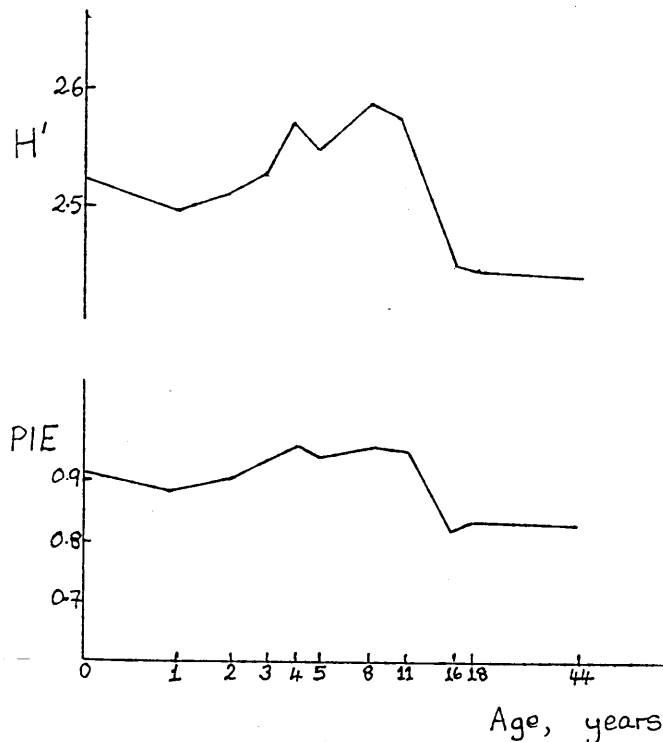


Fig. 2.4

Shannon's measure of diversity H' and Hurlbert's PIE at sites burned at various times in the past (from Shafi & Yarranton, 1973).

Bazzas (1968) studied fields abandoned between one and 40 years ago after corn cultivation (and in one case, soybean cultivation). He found that annual plants dominated the vegetation in the first year after abandonment: annuals are well-adapted to invasion having abundant and often persistent seed, and high growth rates since they must flower and fruit in one year from seed. Bazzas found that perennial plants were dominant over the next few years, and shrubs and trees became dominant after 40 years. Perennials have lower reproduction rates than annuals but are necessarily better adapted for competition since they must occupy a site for longer before

reproducing. Trees and shrubs carry these characteristics even further. Tramer (1975) found this pattern repeated on other abandoned fields; and the species turnover declined with time, demonstrating increasing resistance to invasion.

2.2 vii) Alternative models explaining diversity trends during ecological succession

Competition is not the only mechanism which could cause the observed trend of increasing then slightly decreasing diversity during ecological succession. Connell and Slatyer (1977) present three possible models. The three models agree in their first stage: propagules arrive at random, and the species which become established are those with fast growth and widely-dispersed seeds which are well adapted to the invasion of new territory. The 'facilitation model' says that these species are the only ones able to invade the territory; they modify the environment (perhaps altering soil structure or reducing mineral concentrations) and allow other species, previously unable to invade, to become established. This second group of species in turn modifies the environment, making it suitable for further species, and so on. The 'tolerance model' says that the early-succession species are replaced by species more suited to the environment but slower to become mature; for example, they may be better able to tolerate shade, or lack of water, and thus have a competitive advantage over the pioneer species. This model is roughly equivalent to that described in section 2.2.ii). The 'inhibition model' states that once an individual is established, it is likely to hold its space against potential invaders, but that once it dies its position is

occupied at random by an individual of any other species. Eventually, the longer-living species will dominate the area simply because they are longer-living and replaced less often. The second and third models would predict that the highest diversity occurs in the middle period, when first-succession species and longer-lived/better competition species temporarily coexist. I am not sure that the 'facilitation model' makes any predictions about diversity.

Such evidence as exists (see Connell & Slatyer for discussion) suggests that the 'facilitation model' may apply in the early stages of invasion of newly-exposed surfaces (for example, the colonization of sand-dunes). It is more difficult to distinguish between the 'tolerance' and 'inhibition' models. Evidence for the 'inhibition model' consisting of observations that early species inhibit the growth of later ones can equally apply to the 'tolerance model': a species can inhibit the growth of a superior competitor yet eventually succumb. More convincing is evidence on these lines: in abandoned fields in Oklahoma, an annual species of grass persisted for up to 15 years before being replaced by a perennial species of bunchgrass (Booth, 1941) that was less tolerant of low levels of phosphorus and nitrogen (Rice et al, 1960); Rice et al went on to show that at nearly every combination of levels of nutrients, the annual grass grew more rapidly than the perennial, making it unlikely that the perennial became dominant by direct competition. Unless the perennial was more tolerant than the annual of some other deficiency of the habitat, the 'inhibition model' would seem to apply.

The 'tolerance model' need not imply the direct competition of section 2.2ii): Sousa (1979) gives an example of algal succession on a boulder-strewn shore in California where the eventual dominant replaces earlier species not as a result of direct competition but because of resistance to dessication and epiphytes.

2.2 viii) Lowered diversity in extremely predictable environments

We have seen that the theory of diversity changes during succession predicts a final decrease in diversity. Similarly we would expect the most stable environments to support communities that are less diverse than those in environments which are less predictable, where fluctuations periodically reduce species numbers and in effect return succession to an earlier stage. This hypothesis is one of those presented by Connell (1978) who calls it the 'intermediate disturbance' hypothesis. When disturbances to the community are frequent, only species well-adapted to recover quickly will survive, and diversity will be low. At the other extreme, when the environment is very predictable, the most efficient competitors or the longest-lived species will dominate, and diversity will continue to decline until a disturbance in the environment kills many individuals and creates space for individuals of other species. Thus the greatest diversity is expected at intermediate frequencies of perturbation.

Huston (1979) further developed the idea that high diversity is maintained when the community is prevented from reaching a competitive equilibrium, and he pointed out that the frequency of perturbation must be considered relative to the rate of movement of the community towards equilibrium.

2.2 ix) Evidence supporting the 'intermediate disturbance' hypothesis

Total predictability is unlikely in natural habitats, so direct evidence for the final decrease in diversity is hard to come by. Connell cited the work of Egge (1947), who observed 75%-90% domination by Ironwood (Cynometra alexandrei) of undisturbed rainforest in Uganda. Sale (1977) pointed out that although coral reefs have a high diversity of fish species, within

the same habitat type coral reef fishes on the whole do not show extreme specialization, and highly specialized species often coexist with other species showing the same specialization. However, living space on the reef is subject to unpredictable changes because of wave action, silting and sand shifting, and, on a larger scale, cyclonic storms. Predation acts to increase living space for the remaining fish. Sale suggested that this unpredictability is the reason for the high diversity.

2.2 x) Disagreement over the importance of competition in determining community structure.

The 'inhibition model' of Connell & Slatyer (section 2.2 vii) makes no use of direct competition as a factor in succession. It is possible too that competition is not as important a mechanism for increasing diversity as has been believed. Strong et al (1978) modelled the invasion of new territory by random invasion of species from those available in surrounding areas. They ranked by wing length and culmen size birds of the same family in the Tres Mariás Island, Mexico, and the California Channel Islands, USA, and found that the ratio of measurements of adjacently ranked species were no larger than expected from the model of random invasion. Larger ratios than expected would indicate avoidance of competition by specialization. They reached similar conclusions for the finches of Galapagos. Since observation of this 'character displacement' has been an important factor in the belief that competition plays a large part in determining community structure, Strong's demonstration that in three cases apparent character displacement can be explained by purely random behaviour suggests competition may not play such an important part after all. Further evidence that this may be so comes from recent work on mathematical models. Armstrong & McGehee (1980)

demonstrated that, contrary to widely-held belief, n species can coexist in persistent cycles on fewer than n resources. Sale & Dybdahl (1975) experimented with artificially placed pieces of coral reef. They found no evidence of mutually exclusive pairs of species and no evidence that species were partitioning the habitat either by time or by space. Thus establishment of a particular species appeared to be a matter of chance, rather than of competitive advantage.

2.2 xi) Conclusions

Many attempts have been made to explain the establishment of a community as the result of competition between species, in relation to the predictability of the environment. More recently it has been suggested that competition may not play such an important part; indeed, that apparently structured community development may result by pure chance. Strong et al (1978) pointed out that until we have rejected the possibility of a community having developed by a random process, there is little point in hypothesising a non-random mechanism for its development.

Nevertheless, whether as a result of random events or by a well-structured procedure of competitive interactions, it appears that the species best-fitted to a particular habitat eventually succeed; and that the highest diversity occurs at an intermediate point in this succession, before less well-fitted species have been excluded.

2.3 Diversity and community stability

2.3 i) Introduction

I have discussed the question of what sort of conditions are likely to produce a diverse community. There is a converse to this question: is a diverse community more or less stable than a non-

diverse one, and does it therefore require more or less specialized conditions for its persistence? A common desire in countryside planning is to preserve diversity, partly because a high diversity of plant and animal species is interesting in itself, but also because it may be believed that a diverse community is better able to withstand the pressures that man imposes upon it. The reasoning is this: in a complex community with many species and many interactions between species, there are many alternative energy pathways available. A predator accustomed to eating many species is less affected by the extinction of one of these species than is a predator whose sole food source was that species. Elton (1958) summarised the reasons for considering that complex systems are more stable, less subject to destructive oscillations, and less vulnerable to invasions:

- 1) Single species predator-prey models predict large fluctuations in abundance.
- 2) Simple laboratory cultures of one or two species are usually unstable.
- 3) Natural habitats on small islands seem to be more vulnerable to invasions than those on continents.
- 4) Outbreaks of one species are commoner on cultivated land, and are more serious when only one species is grown. Outbreaks do not occur in the diverse and complex tropical forest.
- 5) Numerical stability is greater in tropical forest than in sub-arctic areas with relatively few abundant species.

However, these arguments can be disputed. Recent work on mathematical models (May, 1974c) shows that more complex models are in fact less stable than the corresponding simple models.

Simple laboratory cultures tend to lead to extinctions, but are complex communities any easier to keep in the laboratory? Hairston et al (1968) have found that laboratory cultures of Paramecia cannot be shown to last longer when they have three species rather than two. In any case, it is difficult to apply the results of laboratory experiments to large natural communities.

It seems reasonable that it is more difficult to invade a large land area because large land areas support more species than small islands and thus are more likely already to contain possible predators of the invading species. However, there are counter examples - European Gypsy moth in America and Opuntia in Australia are examples of successful invasions of larger continents.

It would seem easier for a pest of a single species to 'explode' in a monoculture, or to invade a non-diverse habitat, because of the difficulty of transferring from one food item to another. But providing the food items are not scattered so far apart that transport between them is impossible, the presence of intervening species seems irrelevant. There were few elm monocultures in England, yet this did not prevent the almost total killing of elm trees in the southern and western counties of England during the Dutch Elm Disease outbreak of the 1970's. And there are many instances of persistent natural monocultures, for example, the marsh grass Spartina, mussel beds, bracken and gorse.

The apparent differences in numerical stability between tropical forest and sub-arctic areas may be more in the literature than in fact. Fluctuations in species numbers (such as the well-documented hare and lynx example in Northern Canada) are more obvious when diversity is low. If there are many species, each may be fluctuating wildly yet the overall effect may be of constant numbers, and this may be true for tropical forests.

2.3 ii) Mathematical definition of stability

Before we consider this question any further, we must consider what we mean by stability. Orians (1975) and Whittaker (1975), amongst others, have given summaries of the many different meanings that can be assigned to the word 'stability'. Not all these definitions are particularly useful in the present context. Any ecosystem will be subject to stochastic fluctuations in numbers arising from the random births and deaths of individuals. For a system to persist, it must be capable of returning to a steady state after small deviations in numbers from the steady state position. The traditional mathematical concept of stability is the ability of the system to return to its equilibrium position after a small disturbance to the abundance of the species - the addition or removal of one or two individuals. This type of stability can be investigated mathematically. May (1973) has analysed the stability of mathematical models as follows:

Suppose the abundance of the S species are represented by $\underline{N} = (N_1, \dots, N_S)^T$. Then the system can be represented by a set of differential equations representing the dependence of each species on every other species:

$$\begin{aligned} \frac{dN_1}{dt} &= f_1(N_1(t), \dots, N_S(t)) \\ &\vdots \\ &\vdots \\ &\vdots \\ &\vdots \\ \frac{dN_S}{dt} &= f_S(N_1(t), \dots, N_S(t)) \end{aligned} \tag{2.1}$$

where the f_i are functions of the N_i .

If some value of \underline{N} , say $\underline{N}^E = (N_1^E, \dots, N_S^E)$ can be found such that \underline{N}^E does not vary over time (in 2.1), $\frac{dN_1}{dt} = \dots = \frac{dN_S}{dt} = 0$, then \underline{N}^E is an equilibrium point of the system.

Near the equilibrium point, the system may be represented as a set of linear equations. Consider a small disturbance about the equilibrium point:

$$N_j(t) = N_j^E (1 + v_j(t)) \quad j = 1, \dots, S \quad (2.2)$$

Substitute (2.2) into (2.1) and expand by the Taylor series neglecting terms in v_j^2 and higher powers:

$$\frac{dv_j(t)}{dt} = a_{jk} v_k(t) \quad (2.3)$$

where

$$a_{jk} = \frac{N_k^E}{N_j^E} \left(\frac{\partial f_j}{\partial N_k} \right)^E \quad (2.4)$$

(this is a set of linear equations for v_j)

The a_{jk} measure the effect of the k^{th} species on the j^{th} species near the equilibrium position.

Write

$$v_j(t) = \sum_{k=1}^S \beta_{jk} e^{\lambda_k t} \quad (2.5)$$

The β_{jk} are constants depending on the initial conditions. The S constants λ_k are found by substituting (2.5) into (2.3) to obtain:

$$\lambda v_j(t) = \sum_{k=1}^S a_{jk} v_k \quad (2.6)$$

or equivalently, in matrix notation,

$$(\underline{A} - \lambda \underline{I}) \underline{v} = \underline{0} \quad (2.7)$$

which possesses a non-trivial solution if and only if

$$\det(\underline{A} - \lambda \underline{I}) = 0 \quad (2.8)$$

If λ_j is complex, say $\lambda_j = a_j + bi$, then

$$e^{\lambda_j t} = e^{a_j t} (\cos(b_j t) + i \sin(b_j t)) \quad (2.9)$$

So from (2.5) and (2.9) we see that the imaginary part of the eigenvalue contributes a cyclic term to the expression for v_j .

For the perturbation to die away in time (for $v_j(t)$ to decrease with time) all the real parts of the eigenvalues of \underline{A} must be negative. The matrix \underline{A} , whose eigenvalues describe the nature of the equilibrium, is known as the community matrix.

2.3 iii) Diversity and mathematical stability

May (1974a) demonstrated that stability is not a mathematical consequence of high species richness. For example, consider the two-species Lotka-Volterra predator-prey model:

$$\begin{aligned} \frac{dH(t)}{dt} &= H(t) (a - \alpha P(t)) \\ \frac{dP(t)}{dt} &= P(t) (-b + \beta H(t)) \end{aligned} \quad (2.10)$$

where H is the abundance of the prey (herbivore) and P is the abundance of the predator.

The equilibrium position is

$$\begin{aligned} H^E &= b/\beta \\ P^E &= a/\alpha \end{aligned} \quad (2.11)$$

The community matrix is

$$\underline{A} = \begin{pmatrix} 0 & -\frac{\alpha b}{\beta} \\ \frac{\beta a}{\alpha} & 0 \end{pmatrix} \quad (2.12)$$

with purely imaginary eigenvalues

$$\lambda = \pm i (ab)^{1/2} \quad (2.13)$$

Thus we have purely neutral stability, the displaced community

tending neither to return nor to move further away from the equilibrium position.

May continues to consider the system with $2S$ species:

$$\frac{dH_i(t)}{dt} = H_i(t) \left(a_i - \sum_{j=1}^S \alpha_{ij} P_j(t) \right) \quad (2.14)$$

$$\frac{dP_i(t)}{dt} = P_i(t) \left(-b_i + \sum_{j=1}^S \beta_{ij} H_j(t) \right) \quad i = 1, 2, \dots, S$$

The community matrix is a $2S \times 2S$ matrix partitioned into 4

$S \times S$ blocks:

$$\underline{A} = \begin{pmatrix} \underline{0} & \underline{\alpha}^E \\ \underline{\beta}^E & \underline{0} \end{pmatrix} \quad (2.15)$$

with:

$$\begin{aligned} \underline{\alpha}^E &= (\alpha_{ij})^E; & \alpha_{ij}^E &= H_i^E \alpha_{ij} \\ \underline{\beta}^E &= (\beta_{ij})^E; & \beta_{ij}^E &= P_i^E \beta_{ij} \end{aligned} \quad (2.16)$$

where the superscript E denotes the value at equilibrium.

The $2S$ eigenvalues occur in S pairs of complex numbers:

$$\lambda = \pm (\xi + i \zeta) \quad (2.17)$$

Therefore, either all the eigenvalues have real parts zero (neutral stability as before), or at least one eigenvalue has real part positive and the system is unstable. Thus for a purely random choice of parameters, the multispecies model is less likely to be stable than the one predator-one prey model.

This is an interesting result since, as May (1974c) pointed out, equations of the Lotka-Volterra type faithfully characterise the stability properties of a much wider class of models.

Strobeck (1973) has demonstrated that for S competing species (in a system described by Lotka-Volterra type equations) to exist in stable equilibrium, $2(S - 1)$ inequalities must be satisfied. Thus, for a random choice of parameters, an increase in the number of species decreases the chance of a stable equilibrium.

2.3 iv) Experimental evidence relating diversity to mathematical stability

Murdoch, Evans & Peterson (1972) showed that, of three abandoned fields, the most diverse field had the greatest alteration in insect abundances from year to year, which the authors interpreted as showing a negative relationship between diversity and mathematical stability.

2.3 v) Ability of a system to withstand a changing environment

Mathematical stability gives us an indication of which ecosystems will persist, suggesting that few-species systems are likely to be more stable, and thus goes some way to explaining why a community has as few or as many species as it has. But we are mainly interested in which communities will survive when the environment is subject to fluctuation. Though tropical rainforests are the most diverse of the world's ecosystems, evidence such as the damage done by the slash-and-burn technique of agriculture suggests that these forests may be highly sensitive to perturbation in the environment. Therefore I am interested in a definition of stability that measures the ability of the community to withstand changes in the environment.

Although a natural community may not be at equilibrium, many communities are changing slowly enough for consideration of the stability of a hypothetical community at equilibrium to be a first step in understanding the stability properties of natural communities.

2.3 vi) Resistance to shock

The shock to the environment may be such as to provide only a

temporary change to the environment. In this case, the effect will be to change the species abundance by a large amount, and the stability of the community may be shown in one of two ways. Firstly, there is the resistance of the community to environmental shock. This is shown by how much the community is disturbed by the shock, by measuring for example how the species abundances change, or changes in productivity, or in species diversity - and is the basis of much experimental work (see section 2.3 iv). Secondly, stability may be shown by the ability of the system to return to the equilibrium position after a large disturbance to the species abundances. This is known mathematically as global stability, or in biological terms as resilience.

2.3 vii) Global stability

A system has global stability if it returns to the same equilibrium point no matter how large the disturbance from equilibrium. If the equations describing the system are linear, any equilibrium position will be unique, so if the equilibrium is stable the system will be globally stable. But it is unlikely that a natural system will be at all realistically described by a set of linear equations. For a system described by non-linear equations to be globally stable within a region R , there must exist a Lyapunov function V of the N_i ; i.e., a function $V(N_1, \dots, N_s)$ such that V is positive definite and $\frac{dV}{dt}$ is negative semi-definite throughout R (an analogy in mechanics is potential energy). However, there is no simple way of finding whether such a function exists for a particular system, or of determining its form if it does exist.

2.3 viii) Structural stability

Alternatively, the shock to the environment may be such as to cause a permanent change to the environment. The ecosystem can be

described by a mathematical model whose parameters represent the interactions between the species. If the environment changes, the change will be more favourable to some species than to others - a species will become more successful in competition with some species and less so with others - and these effects will be reflected in changes in the parameters of the model describing the system. If, when the parameters of the model describing the community change slowly in a continuous manner, the species numbers change in a consistent and continuous manner, then the system is structurally stable; if the species numbers fluctuate in a wild fashion, the community is unstable. An example of a structurally unstable system is the system described by the Lotka-Volterra predator-prey equations with a second order term:

$$\begin{aligned}\frac{dN_1(t)}{dt} &= r_1 N_1 - k_1 N_1 N_2 - d_1 N_1^2 \\ \frac{dN_2(t)}{dt} &= k_2 N_1 N_2 - r_2 N_2 - d_2 N_2^2\end{aligned}\tag{2.18}$$

where N_1, N_2 are the abundances of species 1 and species 2, r_1, r_2, d_1, d_2, k_1 and k_2 are constants. If $d_1 = d_2 = 0$ there is neutral stability and the two species undergo undamped oscillation, travelling in closed circles in the N_1, N_2 plane (see Fig. 2.5a). However, if $d_1, d_2 \neq 0$ there is a stable equilibrium position provided that $r_1/d_1 > r_2/k_2$, and N_1 and N_2 spiral inwards; and if $r_1/d_1 < r_2/k_2$ the predator goes extinct (see Fig. 2.5b).

This is an interesting theoretical concept but not of much practical use. We are interested in the more general case where the nature of the equilibrium is not changed, but the position of the equilibrium position is changed.

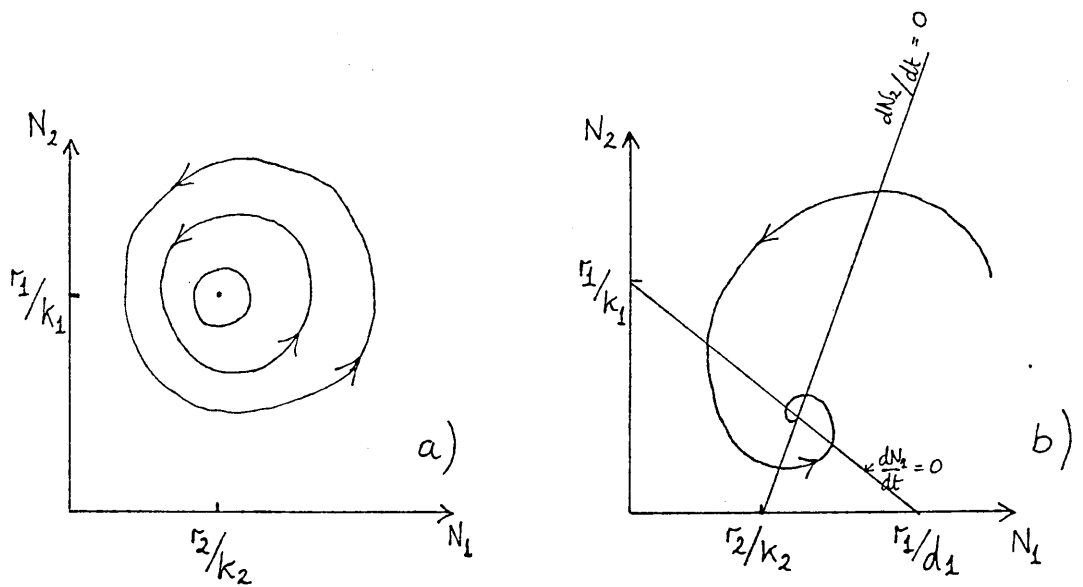


Fig. 2.5

Structural instability of Lotka-Volterra model.

It is difficult to investigate this type of stability using mathematical models. We need to alter all the parameters by some small amount (and altering all the parameters by the same proportion may not alter the equilibrium position). Then there are two ways in which instability may show itself. The equilibrium position may change discontinuously when the change in parameters is continuous. Since even the simplest models give rise to complicated formulae for equilibrium positions, it is impractical to look at the dependence of the change in equilibrium position on the change in parameters. We can instead attempt to find if a 'small' change in parameters causes a 'large' change in equilibrium position, but then we have the problem of defining large and small in two different metrics.

Alternatively instability may reveal itself by the system not reaching the new equilibrium position, or approaching it rather slowly. This is easier to investigate: we may alter the parameters to give a new equilibrium position and watch the progress of the system to this new position. This is most easily done by computer

simulation and forms the basis of the experiments described in Chapter 3.

2.3 ix) How to recognise resistance in practical experiments

The argument on whether complexity of the community causes instability in conditions of environmental change is related in part to a lack of agreement on how to recognise resistance. McNaughton (1977) discussed resistance of grasslands to the impact of African buffalo grazing and concluded that while the more diverse plant community was subject to a greater diversity modification by grazing, there was a smaller effect on functional properties (maintenance of total green biomass) in the less diverse stand. McNaughton considered the alternative views of stability - in terms of diversity change and in terms of functional response - and was firmly of the opinion that the latter is the property of interest. McNaughton gave another example - the effect of a nutrient pulse on two abandoned fields - where again one is led to contrary conclusions by considering diversity or productivity and biomass. So it does seem that we must choose between the two. While total green biomass is of interest when one is considering grazing animals which have no food preference, I feel that generally one is interested also in the variety of plants present - that they are of different kinds, not all one type of organism 'green plant'. So I feel that consideration of diversity modification is of more general interest, although it is better to use some more direct measure of the similarity between the abundances before and after the shock.

There is a shortage of experimental evidence relating resistance to stability. Hurd & Wolf (1974) considered the effect of a nutrient shock (a single application of fertilizer) on fields which had been abandoned since different dates, and which had different diversities,

but they were interested in the effect on productivity, as were Mellinger & McNaughton (1975), rather than the effect on species numbers. Bakelaar & Odum (1978) were more interested in whether a nutrient shock 'sets back' a community to an earlier level of succession.

2.3 x) Studies relating global stability to diversity

The relationship of diversity to global stability - the ability of a community to return to normal after a shock - requires study over a longer period than for the relationship of diversity to the amount of disturbance, since the study cannot be terminated until at least some of the communities involved have returned to normal. It is hardly surprising therefore that the experimental evidence on this aspect of diversity is limited. Boesch (1974) discussed one example. He compared the slow recovery from pollution in the diverse York estuary, Virginia, with the rapidity with which man-made ponds in a less diverse Chesapeake Bay location developed a community similar to that of the surrounding area.

But to be convincing, a study which isolates the ability of a system to return to normal from any other aspect of diversity should involve deviations from equilibrium that are in some sense equal - a difficult thing to arrange in natural communities.

2.3 xi) The nature of the temporary change to the environment

In the event of a catastrophe - a forest fire, the release of noxious chemicals - the effects of the shock on the individual species present will override any effect on the community as a whole. Thus we should investigate the effect of changes to the environment that are larger than the random fluctuations that the community is usually subject to, but which are not so large as to have the effects of a 'catastrophe'.

Larsen (1974) gave an account of an influx of fresh water into the James River estuary, Virginia, after the tropical storm Agnes. The more diverse down-estuary sites suffered more than the less diverse upper estuary, and it is tempting to regard this as evidence that diversity does not bestow resistance. But it is to be expected that an influx of fresh water will have more effect on salt adapted marine creatures than on estuarine creatures living in less salty conditions. This is an effect independent of the diversities of the two communities. Consider also an unpredictable environment. The unpredictability allows only generalist species to exist, and they by their nature will be tolerant of changes in the environment, whereas a predictable environment will be inhabited by specialists which will not be able to survive a changing environment. Thus an observed link between diversity and stability may not be a causal link. From these two examples we see that the shock must be unrelated to any initial differences in the communities to be compared. In particular we have to establish not only whether a diverse community is less able to withstand environmental shock than a non-diverse one, but also whether this is because of the nature of the species involved (whether specialist or generalist) or whether it is because complexity in itself bestows instability.

2.3 xii) Conclusions

The forms of stability of most interest are the resistance to change following a temporary change to the environment, the ability of the system to return quickly to equilibrium after such a change, and the ability of the system to move directly and smoothly to a new equilibrium position following a permanent change to the environment. These three aspects of stability are difficult to analyse mathematically, and must be approached by computer simulation, by experiment or by

observation of natural systems. Observation of natural systems provides circumstantial evidence, but so entangled with other effects (see section 2.4 xi) that no clear answers emerge. Direct experimentation faces similar problems. Computer simulation allows us most control over the conditions for the experiment but the relevance of the simulation to natural systems must be established. No single method will solve all the problems; a synthesis of results from all three methods must be considered, and even then success is not assured.

3. Computer simulation experiment to investigate the relationship between diversity and stability

3.1 Introduction

As mentioned in chapter 2, the most feasible way to study the structural stability of a system subject to long-term changes in the environment is by computer simulation of a stochastic model describing the system. A change in the environment can be considered as having the effect of altering the between- and within-species interactions (the environment will become more favourable to some species and less so to others) and can be simulated by changing the parameters of a mathematical model describing the system.

I do not have enough time to carry out a full investigation of the problem, and so I have confined myself to a pilot study involving only two species in order to familiarise myself with the techniques involved and to reveal some of the problems that may arise.

3.2 Choice of model

3.2 i) Number of species

Since the main purpose of this study is to show problems that are likely to arise in this approach, it seems unnecessary to investigate a model with the half-dozen or more species that would be biologically realistic. Even a simple model involving only two species is likely to have at least four parameters representing between- and within-species interactions, and a four species model will have 16-20 parameters. For more species

than this, the problem becomes impossibly cumbersome, since to seek for a general relation between diversity and stability, the experiment will need to cover a wide range of values for every parameter. Maynard-Smith (1974) considers it possible that the extent to which actual ecosystems show mathematical stability depends in part on the extent to which the pairwise interactions between species would in isolation lead to stability. I am inclined to doubt whether this holds for structural stability. Nevertheless, for this preliminary study, I choose the simplest case possible, that of two species.

I shall return later (Section 3.10) to the problems arising when more than two species are involved.

3.2 ii) Type of model used

I have chosen to investigate a competition model for three reasons, firstly, because competition is an important aspect of natural communities, secondly, because predator-prey equations tend to give stable equilibrium cycles rather than stable equilibrium points, and thirdly, because of the symmetry of function of the two species in a competition model, by which I mean that a system with equilibrium position $(30,60)$ can be expected to behave in the same way as one with equilibrium position $(60,30)$, and there is no need to investigate both.

The model I have used is a stochastic model whose deterministic equivalent is the Lotka-Volterra two-species competition model with a self-inhibiting term:

$$\frac{dN_1}{dt} = (a_1 - b_{11} N_1 - b_{12} N_2) N_1$$

(3.1)

$$\frac{dN_2}{dt} = (a_2 - b_{21} N_1 - b_{22} N_2) N_2$$

where N_1 and N_2 are the abundances of the two species

a_1 and a_2 represent the birth rates of species

1 and species 2

b_{11} and b_{22} give the death rates of species 1 and

species 2 in the absence of the competitor (the

self-inhibiting term)

b_{12} and b_{21} are death rates due to competition

The system has an equilibrium position at

$$N_1^E = \frac{a_1 b_{22} - a_2 b_{12}}{b_{11} b_{22} - b_{12} b_{21}}$$

(3.2)

$$N_2^E = \frac{a_2 b_{11} - a_1 b_{21}}{b_{11} b_{22} - b_{21} b_{12}}$$

where $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$

given by the intersection of the two lines

$$a_1 - b_{11} N_1 - b_{12} N_2 = 0$$

$$a_2 - b_{21} N_1 - b_{22} N_2 = 0$$

(3.3)

(see figure 3.1)

For a stable equilibrium position at which both species are present we require

$$\frac{a_1}{b_{12}} > \frac{a_2}{b_{22}} \quad \text{and} \quad \frac{a_2}{b_{21}} > \frac{a_1}{b_{11}} \quad (3.4)$$

(see figure 3.1 and Maynard-Smith, 1974)

$$\text{or} \quad \frac{b_{11}}{b_{21}} > \frac{a_1}{a_2} > \frac{b_{12}}{b_{22}} \quad (3.5)$$

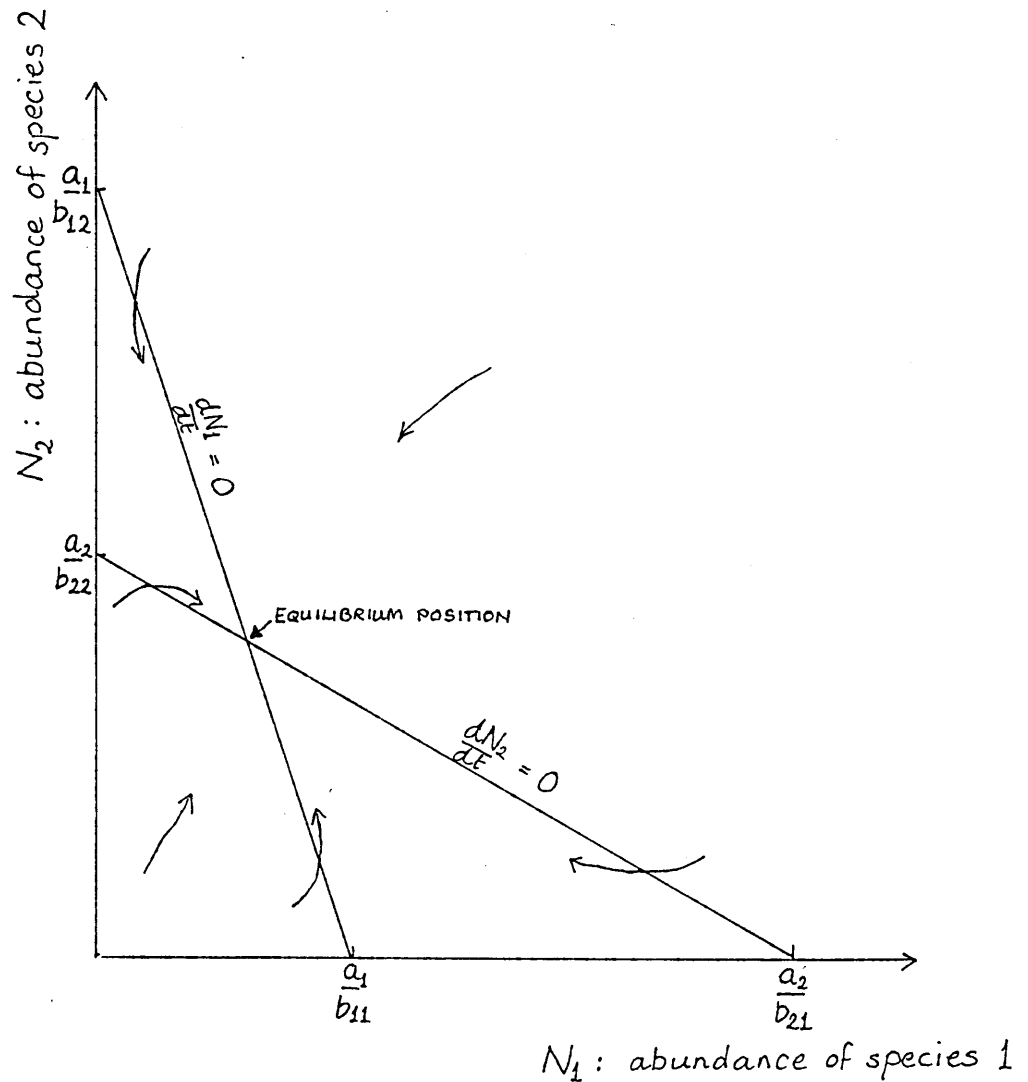


Figure 3.1

Equilibrium position for the Lotka-Volterra competition model

This model is not entirely realistic although it has been shown to describe well some natural systems, for example, yeasts (Slobodkin, 1962). However, the reason for its use here is not because it describes accurately a real situation, but because it contains the general characteristics of competition between two species. The number of births of species 1 is proportional to the number of individuals of species 1. On its own, this gives exponential growth, and so the model includes a term for deaths due to competition between individuals of species 1, with the number of deaths proportional to N_1^2 .

This death rate will be larger than the birth rate for sufficiently large values of N_1 . Finally, the number of deaths due to competition with species 2 is proportional to the product $N_1 N_2$.

The equation describing the behaviour of species 2 is interpreted similarly.

The stochastic model is as follows

Probability of a birth in species 1 in the small time interval $(t, t + \delta t)$ is $(a_1 N_1) \delta t + o(\delta t)$

Probability of a death in species 1 in $(t, t + \delta t)$ is $(b_{11} N_1^2 + b_{12} N_1 N_2) \delta t + o(\delta t)$

Probability of a birth in species 2 in $(t, t + \delta t)$ is $(a_2 N_2) \delta t + o(\delta t)$

Probability of a death in species 2 in $(t, t + \delta t)$ is $(b_{21} N_1 N_2 + b_{22} N_2^2) \delta t + o(\delta t)$

The computer program to generate this model incorporates a random number generator to determine the time of the next event and its type - birth in species 1, etc.

3.2 iii) Simulating environmental change

The change in the environment is simulated by changing the parameters of the model (see section 3.1).

I consider the effect of a single substantial but not too large change in the parameters. Too small a change will have negligible effect on the system, being masked by stochastic variation in the model, whereas there is little point in choosing a really large change in the parameters since, as already discussed (section 2.3 xi) a large shock to a natural environment probably needs to be considered in terms of its effect on each individual species. A change somewhere between these two extremes is required, although the exact value is somewhat arbitrary. I have chosen the new parameters by considering a new equilibrium position not too far removed from the old and calculating the parameters required to give this new equilibrium position. This allows a more systematic approach to the investigation than does altering the six parameters in the model without reference to the physical meaning of the alteration.

3.3 Form of the simulation problem

The simulation problem takes this form:

The species numbers fluctuate randomly about the equilibrium position. Change in the environment is simulated by change in the parameters of the model; the new parameters define a new equilibrium position. The community will move towards the new equilibrium position - the speed with which it does so may depend on the diversity of the community before the change of parameters, and this is what I want to investigate.

Since the path to the new equilibrium point depends only on the starting point, and not on the history of the community, I need only study the system from the point where the parameters change.

The new equilibrium position must be stable in the mathematical sense. If it were unstable, then by definition a community displaced from the equilibrium position would tend to move further away, and would therefore never reach the new equilibrium.

Therefore, I need to define a stable 'new' equilibrium position, and a starting point not too far removed from it representing the state of the community at the time when the environment changed. The magnitude of change to the environment is to some extent reflected in the difference between the starting point and the new equilibrium position.

3.4 Factorial design I for simulation studies

3.4 i) Factors

I wish to see how diversity affects stability under different changes in the environment. It seems advisable to see how any relationship varies in different sized communities. Therefore I need as factors the total number, N , of individuals in the community (community size); diversity, R , which for two species is equivalent to the ratio $N_1:N_2$; and change in environment, which may be considered as two factors, change in diversity, DR , and change in community size, DN .

The factor levels are:

Ratio R	1:1	1:2	1:4
Community size N	30	60	120
Change in ratio DR	x0.5	x2	
Change in community size DN	x0.5	x2	

3.4ii) Response

With a stochastic model, it is unrealistic to require that the community should reach the new equilibrium position exactly. All we require is that the community should be sufficiently close to be within the region likely to be covered by random fluctuation about the new equilibrium position. We therefore need to define a distance between the point (N_1, N_2) representing the two species and the new equilibrium position (N_1^E, N_2^E) . The obvious measure of distance is the Euclidean distance

$$d = \sqrt{(N_1 - N_1^E)^2 + (N_2 - N_2^E)^2} \quad (3.6)$$

But this distance does not take into account the different speeds and directions of movement implied by the deterministic model in different regions of the species space. In particular there are strong edge effects; near each axis the movement is parallel to the axis. So a better approach is as follows:

The probability that the point (N_1, N_2) is drawn from a bivariate Poisson distribution with mean (N_1^E, N_2^E) has log-likelihood

$$L = N_1 \log\left(\frac{N_1}{N_1^E}\right) + N_2 \log\left(\frac{N_2}{N_2^E}\right) - N_1 - N_2 + N_1^E + N_2^E \quad (3.7)$$

and $2L$ has the χ^2 distribution on 2 d.f. It seems reasonable to assume that the population has reached the new equilibrium position as soon as:

$$2L < \chi^2(95\%) \approx 6$$

A suitable response is the ^{logarithm of the} time taken to reach $2L \leq 6$

The rate of events at the starting point is not constant throughout the experiment :

$$\text{Rate of events at starting point} = r \frac{N_1}{N_1^E} \left(1 + \frac{l N_1 + N_2}{l N_1^E + N_2^E} \right) + r \frac{N_2}{N_2^E} \left(1 + \frac{m N_1 + N_2}{m N_1^E + N_2^E} \right)$$

where r = rate of events at equilibrium

l = gradient of $\frac{dN_1}{dt} = 0$

m = gradient of $\frac{dN_2}{dt} = 0$

Though independent of N , since N_1, N_2, N_1^E and N_2^E are all proportional to N it depends on DN , being much larger for $DN = 0.5$ than for $DN = 2$ (see table 3.1). A second response, designed to counteract this effect, is the logarithm of the number of events before $2L \leq 6$

	R = 1:1		R = 1:2		R = 1:4	
$\frac{DN}{DR}$	0.5	2	0.5	2	0.5	2
0.5	3.6	0.44	3.1	0.38	2.7	0.34
2	3.6	0.44	4.1	0.49	4.3	0.52

Table 3.1

Theoretical rate of events at the starting point for model I

The two responses are

- 1) the log to base e of the time taken for the system to reach the neighbourhood of the new equilibrium position (LT)
- 2) the log to base e of the number of events before the system reaches the neighbourhood of the new equilibrium position (LE)

3.4 iii) Number of replications

There are 3 replications

3.4 iv) Factors held constant

To try to ensure that the behaviour in the region of the equilibrium position is the same throughout the experiment, I keep constant the gradients of $\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$ at -4 and -0.25 respectively. This gives the conditions:

$$\frac{b_{11}}{b_{12}} = 4 \quad (3.8)$$

$$\frac{b_{21}}{b_{22}} = 0.25$$

I also keep constant at 0.25 the probability at equilibrium of a birth in either species (so that the time taken to reach the new equilibrium point as far as possible depends only on the four factors of interest). Thus:

$$a_1 N_1^E = 0.25 = a_2 N_2^E \quad (3.9)$$

3.4 v) Procedure adopted

The conditions (3.2), (3.8) and (3.9) are sufficient to define the six parameters for a given choice of equilibrium position.

So the method is:

- 1) Choose the starting point and new equilibrium position.
- 2) Use equations (3.2), (3.8), and (3.9) to find the values of the parameters a_i and b_{ij} .
- 3) Simulate the approach to equilibrium and measure the number of events and the time taken.

3.5 Results and analysis

3.5 i) The problem of extinction

It is difficult to know how to approach the problem of extinction. On the one hand, extinction is an extreme form of

instability, and we could try to incorporate such a result by arbitrarily assigning it a very large response time, say, $LT = 100$. But my variables are designed to measure how rapidly the system reacts to the change of equilibrium, and some of the communities in which one species became extinct were performing rather well in this respect, as shown by a plot of χ^2 distance against log time. Figure (3.2) shows χ^2 distance against log time for $N = 60$, $R = 1:4$, $DN = 0.5$, $DR = 2$. Although one of the species became extinct before $2L \leq 6$, there was a steady reduction in χ^2 distance before this occurred. It seems that extinction is a separate aspect of the problem, and so I have chosen to regard extinctions as missing values.

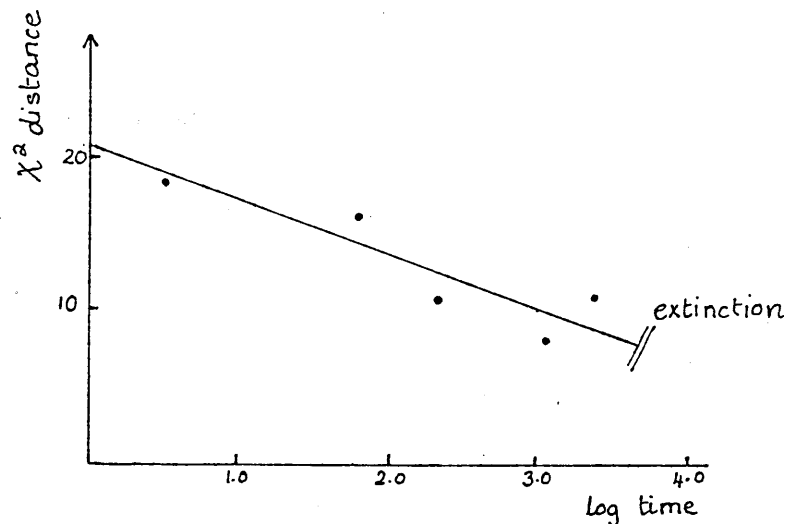


Figure 3.2

χ^2 distance vs log time for $N = 60$, $R = 1:4$, $DN = 0.5$, $DR = 2$.
(Position plotted after every 10 events)

3.5 ii) Results: LT

The log first passage time LT averaged over the three replications is shown in Table 3.2, and the two-way table of means for $R \times DR$ in Table 3.3.

R	<u>DN = 0.5, DR = 0.5</u>			<u>DN = 0.5, DR = 2</u>		
	1:1	1:2	1:4	1:1	1:2	1:4
N						
30	1.3	1.9	2.5*	1.0	2.2	1.6
60	3.3	3.5	3.0	2.9	3.3	2.6*
120	4.2	4.2	5.4	4.1	4.5	4.9*
R	<u>DN = 2, DR = 0.5</u>			<u>DN = 2, DR = 2</u>		
	1:1	1:2	1:4	1:1	1:2	1:4
30	5.1	4.9	4.9	4.8	5.7	5.2
60	6.5	6.2	6.1	6.0	6.5	6.6
120	7.3	7.1	6.9	7.0	7.3	7.6

Table 3.2

Log first passage time averaged over replications. Model I

(Results marked * are based on two replications only because of extinction before $2L \leq 6$ was reached).

R	1:1	1:2	1:4	
DR				
0.5	4.62	4.64	4.94 ₍₁₇₎	4.73
2	4.28	4.92	4.88 ₍₁₆₎	4.69
	4.45	4.78	4.91	4.71

Table 3.3

Two-way table of means for R x DR. Model I

Source	df	ss	ms	F
DR	1	.03	.03	
DN	1	256.7	256.7	1166.6***
R	2	2.6	1.3	5.9**
N	2	106.6	53.3	242.3***
DR.DN	1	1.3	1.3	5.8*
DR.R	2	1.7	0.9	3.9**
DR.N	2	0.9	0.4	2.0
DN.R	2	0.1	0.06	
DN.N	2	2.4	1.2	5.5*
R.N	4	2.9	0.7	3.3*
residual	85	18.3	0.22	
Total	104	393.4		

Table 3.4

Analysis of variance for LT, Model I

From Table 3.3 we see an increase in LT with decreasing diversity.

The analysis of variance is shown in Table 3.4. Although all the main effects except DR are significant, it is immediately obvious that the main difference in LT is caused by the change in numbers DN, and from Table 3.2 we see that DN = 2 gives very much larger values of LT than does DN = 0.5. The χ^2 distance $2L_s$ between

$$L^S = N_1^S \log\left(\frac{N_1^S}{N_1^E}\right) + N_2^S \log\left(\frac{N_2^S}{N_2^E}\right) + N_1^E + N_2^E - N_1^S - N_2^S$$

where (N_1^S, N_2^S) = starting point.

starting point and new equilibrium point is larger for $DN = 2$ than for $DN = 0.5$ (Table 3.5), but it is evident that this difference is not enough to explain the large effect of DN on LT . This difference in χ^2 distance is not as great as the difference in χ^2 distance between $N = 30$, $N = 60$, $N = 120$, although N has a much less significant effect than DN on LT . We must look elsewhere for an explanation of the large effect of DN on LT . The explanation may lie in the rate of events at the starting point, which is independent of N , but which, as mentioned above, is much

R	<u>DN = 0.5, DR = 0.5</u>			<u>DN = 0.5, DR = 2</u>		
	1:1	1:2	1:4	1:1	1:2	1:4
N						
30	15.1	15.0	14.2	15.1	14.5	13.6
60	30.2	30.0	28.4	30.2	29.0	27.2
120	60.5	60.0	56.8	60.5	58.1	54.3
R	<u>DN = 2, DR = 0.5</u>			<u>DN = 2, DR = 2</u>		
	1:1	1:2	1:4	1:1	1:2	1:4
30	21.9	21.8	21.0	21.9	21.3	20.4
60	43.9	43.6	42.1	43.9	42.7	40.8
120	87.8	87.2	84.1	87.8	85.3	81.6

Table 3.5

χ^2 distance at starting point for model I

larger (mean 3.5) for $DN = 0.5$ than for $DN = 2$ (mean 0.44). So we can look instead at the number of events to first passage time.

3.5 iii) Results: LE

The results for the log number of events to first passage (LE) are shown in Table 3.6. Using the response LE reduces the effect of DN to that of N, but these two are still the most important influences on the response.

<u>DN = 0.5, DR = 0.5</u>				<u>DN = 0.5, DR = 2</u>		
R	1:1	1:2	1:4	1:1	1:2	1:4
N						
30	2.9	3.0	3.4*	2.7	3.4	3.0
60	4.3	4.5	3.8	4.0	4.3	3.7*
120	5.1	5.1	5.8	5.0	5.2	5.5*
<u>DN = 2, DR = 0.5</u>				<u>DN = 2, DR = 2</u>		
30	4.7	4.4	4.0	4.4	5.4	4.9
60	6.1	5.7	5.5	5.6	6.3	6.5
120	7.0	6.6	6.4	6.7	7.1	7.6

Table 3.6

LE averaged over replications. Model I (* indicates average over 2 replications only)

3.5 iv) Discussion

I feel that any effect of R would be easier to investigate if we could avoid the large effects of DN and N. None of the chosen responses is independent of DN and there is no obvious sensible way of correcting the χ^2 distance for the differences in DN, and no way of correcting for the different initial rates of events if we choose not to use LE as a response. The best way to carry the investigation further seems to be to keep the initial numbers and the change in numbers constant throughout the experiment.

3.6 Factorial design II

3.6 i) Factors

As before, we have two factors relating to diversity:

Ratio R:	levels	1:1	1:2
Change in ratio DR:		x0.5	x2

Another factor of interest is the behaviour of the system as it approaches equilibrium. This will depend on the gradients of the lines :

$$\frac{dN_1}{dt} = 0 \quad \text{and} \quad \frac{dN_2}{dt} = 0$$

$$\text{gradient of } \frac{dN_1}{dt} = 0 \quad \text{1:levels} \quad -4/3 \quad -4 \quad -12$$

$$\text{gradient of } \frac{dN_2}{dt} = 0 \quad \text{m:} \quad -3/4 \quad -1/4 \quad -1/12$$

3.6 ii) Constant factors

As before, I keep constant the rate of births at equilibrium at 0.25. The initial size of the community is constant at 90, and, as a suitable first experiment, there is no change in numbers between starting point and new equilibrium position.

3.6 iii) The initial χ^2 distance is far more uniform than before (Table 3.7), as is the rate of events at the start (Table 3.8).

R	1:1	1:2
DR		
0.5	10.6	10.2
2	10.6	8.8

Table 3.7

Initial χ^2 distance. Model II

l	<u>R = 1:1, DR = 0.5</u>			<u>R = 1:2, DR = 0.5</u>		
	4/3	4	12	4/3	4	12
m						
3/4	1.14	1.11	1.10	1.01	0.98	0.97
1/4	1.21	1.19	1.18	1.06	1.03	1.02
1/12	1.26	1.24	1.23	1.09	1.06	1.05
l	<u>R = 1:1, DR = 2</u>			<u>R = 1:2, DR = 2</u>		
	4/3	4	12	4/3	4	12
3/4	1.14	1.21	1.26	1.26	1.35	1.43
1/4	1.11	1.19	1.24	1.24	1.33	1.42
1/12	1.10	1.18	1.23	1.24	1.32	1.41

Table 3.8

Rate of events at starting point. Model II

3.7 Results and analysis

3.7 i) Results LT

The results for log first passage time for Model II are shown in Table 3.9, the analysis of variance in Table 3.10, and the two-way table of means for RxDR in Table 3.11. The significant RxDR interaction can be explained by the difference in initial distance and the rate of events at the starting point, both of which seem to show a RxDR interaction (see Tables 3.7 and 3.8). There is a significant effect of DR but no apparent effect of diversity R. The significance of the interactions of R and DR with l are harder to explain because at first sight one would expect the effects of l and m to be similar. It is possible to try to interpret these results by looking at the direction and magnitude of the changes in N_1 and N_2 predicted by the model for different values of N_1 and N_2 . Figure 3.3 shows the situation for a) R = 1:1, DR = 2, l = 4/3, m = 3/4; b) R = 1:2, DR = 2,

1 = 12, $m = 1/12$; and c) $R = 1.2$, $DR = 2$, $l = 4/3$, $m = 1/12$.

The magnitude and direction of the arrows shows the magnitude and direction of the expected motion in the N_1, N_2 plane.

	<u>R = 1:1, DR = 0.5</u>			<u>R = 1:2, DR = 0.5</u>		
1	4/3	4	12	4/3	4	12
m						
3/4	3.3	4.7	5.1	5.4	4.1	4.2
1/4	3.6	4.1	4.3	4.6	3.1	3.6
1/12	3.2	3.8	3.7	3.8	4.0	4.4
	<u>R = 1:1, DR = 2</u>			<u>R = 1:2, DR = 2</u>		
3/4	4.0	4.9	3.5	4.0	3.0	2.5
1/4	3.7	3.7	3.6	3.8	3.5	2.3
1/12	4.0	2.5	4.0	4.8	2.5	1.9

Table 3.9

LT averaged over replications. Model II

⊗ shows the starting point. The community shown in a) has the largest average LT and we see that the starting point is in a region of the N_1, N_2 plane where there is slow motion towards the equilibrium position. Conversely, for the community shown in b) the expected change in numbers at the starting point is very large. The fast change of N_1 relative to N_2 as seen in this diagram is characteristic of systems with $m = 1/12$. By comparison with c), we find that the value of l determines whether the area of large change in N_1 extends as far as the starting point. In this way we can go some way to interpreting the results of Table 3.10; but the picture is not clear-cut and no useful generalisations can be made.

Source	df	ss	ms	F
R	1	1.32	1.32	1.8
DR	1	9.71	9.71	13.2**
l	2	3.54	1.77	2.5
m	2	5.41	2.70	3.8*
R.DR	1	4.04	4.04	5.6*
R.l	2	14.21	7.10	9.9**
R.m	2	0.95	0.47	
DR.l	2	7.94	3.97	5.5*
DR.m	2	0.60	0.30	
l.m	4	2.06	0.51	
higher interactions	16	15.97	1.00	1.40
Treatments	35	65.75	1.88	2.6**
Residual	72	52.08	0.72	
Total	107	117.83		

Table 3.10

Analysis of variance for LT. Model II

R	1:1	1:2	
DR			
x0.5	3.97	4.13	4.05
x2	3.76	3.15	3.45
	3.86	3.64	3.75

Table 3.11

Two-way table of means for R x DR. Model II

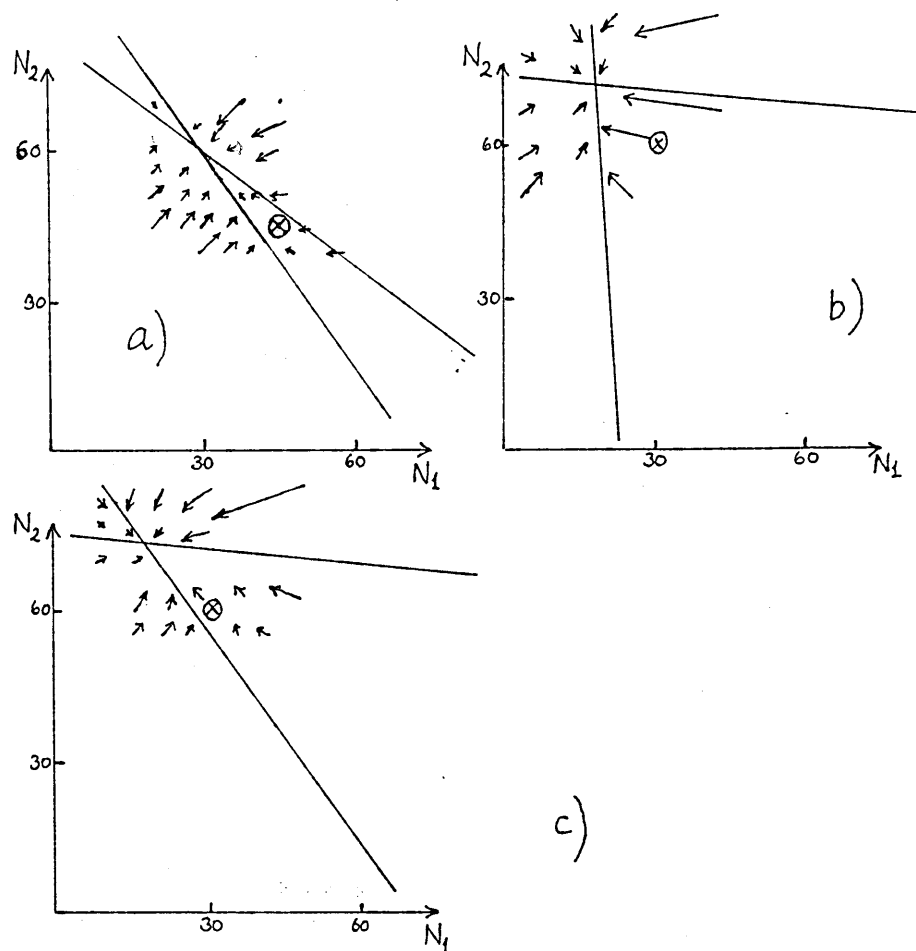


Fig. 3.3

Direction and magnitude of changes in N_1 and N_2 predicted by the model. See text for explanation.

3.7 ii) Results: LE

The results for the number of events to first passage show a similar pattern, but without a large effect for $R \times DR$.

3.8 Discussion of results

Altogether the results of the two experiments are inconclusive as far as our search for a relation between stability and diversity is concerned. However, we have shown some of the problems which can arise. The factors which affect the progress to equilibrium are such things as the rate of events at the starting point, the distance to be travelled, the angle between

the two lines $\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$, and the orientation of these two lines (which can be measured by the slope of the line bisecting this angle) and the position of the starting point relative to these two lines - all things that are very difficult to vary in a systematic manner since their dependence on the parameters of the model is of complicated mathematical form.

3.9 Alternative approach

An alternative approach is to treat this as a regression problem in which we produce variability in the results by altering the model parameters (although for our present purposes these parameters are rather without meaning) and measure the variables which are of interest though difficult to vary in a systematic manner. The variables of most interest are the initial diversity $D_s (= N_1 : N_2)$, the initial χ^2 distance l_s , the rate of events at the starting point R_s , the angle θ between $\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$, and the gradient b_θ of the bisector of this angle, and the position of the starting point relative to the lines $\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$. Since only four factors were varied in the experiment only four of these parameters can be mathematically independent.

The analyses of variance for the regressions of LT and LE on D_s , R_s , θ (using the data of Model II) are shown in Tables 3.12 and 3.13.

Source	df	ss	ms	F
Total	35	21.89		
R_s	1		8.36	20.96**
residual	34	13.53	0.40	
θ adjusted for R_s	1		1.23	3.32
residual	33	12.31	0.37	
D_s adjusted for R_s, θ	1		0.48	1.30
residual	32	11.83	0.37	

Table 3.12

Analysis of variance for regression of LT on R_s , D_s and θ

Source	df	ss	ms	F
Total	35	18.91		
R_s	1		4.48	10.56**
residual	34	14.43	0.42	
θ adjusted for R_s	1		1.68	4.34*
residual	33	12.75	0.39	
D_s adjusted for R_s, θ	1		0.66	1.76
residual	32	12.09	0.38	

Table 3.13

Analysis of variance for regression of LE on R_s , D_s and θ

For LT, the best fit is

$$LT = 8.47 - 3.99R_s$$

Adding further variables gives no significant reduction in the residual ss. Similarly, for LE

$$LE = 7.09 - 2.49R_s - 0.12\theta$$

The important result is that initial diversity does not seem to contribute anything to either response.

3.10 Discussion

As expected, this experiment with two species has not found a mechanism that would give rise to an effect of diversity on stability. But it has shown the problems that can arise (see section 3.8) and has demonstrated that the most fruitful analysis is likely to be a regression model involving all the interesting parameters.

Problems arise when we try to extend this work to more than two species. The χ^2 distance and the rate of events at the starting point extend easily to three or more species. However, a three species community with no predation is unlikely in nature, and so our model should not be a purely competition model; it should include predator-prey interactions. This leads to problems: with three species, there are three between species interactions, and with four species there are six interactions. The direction of the predator-prey interaction must be considered - a situation with 60 prey and 30 predators is rather different from one with 30 prey and 60 predators. These two factors combined give us a large number of models. Since any result, to be of general validity, must be derived from a wide selection of these models the problem is already becoming impossibly large, taking into account the relative strengths of the interactions, which will further multiply the number of cases to be considered. Other aspects of the simulation become similarly complicated; for example, it is more difficult to choose parameters describing the behaviour in the region of the equilibrium position when that equilibrium is the intersection of hyperplanes rather than of straight lines.

Two conclusions arise from this pilot study; firstly, that the complications arising when a realistic number of species is considered are sufficient to make a systematic study impossible; and, secondly, that in any study involving a small number of species and a change in equilibrium that does not involve the extinction of any species, the number of individuals in the community is likely to have far more effect on the stability (as defined here) of the community than does initial diversity of the community.

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